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Floral Ontogeny of Mimosoid Legumes.

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in

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by
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ABSTRACT

Comparative floral ontogeny in mimosoid legumes was analyzed among representative genera in three major tribes Mimoseae, Acacieae and Ingeae. Details on floral and inflorescence ontogeny in one mimosoid species is described and illustrated for Mimosa strigillosa Torr. & Gray. Three features studied developmentally include: variation in number of parts, patterns of arrangement and inflorescence architecture. Suppression occurs along inflorescences that develop synchronously, when basal flowers are retarded. Tetramerous flowers are considered a reduction or suppression from a basic pentamerous flower. Divergent patterns in order of sepal initiation and stamen initiation and proliferation are found during early ontogeny. Four patterns found in the calyx are: helical, simultaneous whorl, bidirectional and ring meristem. Helical is considered primitive and the others derived. Three main types of androecium (haplostemony, diplostemony, multistaminy) were studied developmentally. Four different mechanisms were recognized in the multistaminate androecium: acropetal, lateral, sectorial and helical. Differing patterns in both sepal initiation and stamen initiation occur at non-terminal points in ontogeny. These differences are not reflected in adult morphology due to equalization of size of parts. Since some characters detected during floral ontogeny occur in more than one tribal line it is suspected that parallelisms play a major role in mimosoid evolution.

INTRODUCTION

Mimosoids comprise a group of legumes with wide geographical distribution among continents. Compared to the other subfamilies of legumes (Caesalpinioideae, Papilionoideae), floral morphology of mimosoids is rather simple with generally five-merous flowers, radial symmetry and valvate aestivation.

Comparative floral ontogeny among mimosoids studied in this research is part of an ongoing research on floral ontogeny of legumes at Shirley C. Tucker's laboratory. Representative genera for the study are included in the three major tribes (Mimoseae, Acacieae, Ingeae) in mimosoids.

The main objectives of this research are: 1) to compare divergent patterns of organ initiation and development; 2) to verify the unique position of floral organs in mimosoids, compared to that of other subfamilies; 3) to compare differing developmental patterns which produce stamen proliferation among mimosoids and 4) to determine whether developmental characters are correlated with tribal alignments. Information on developmental pathways of major morphological characters may help to determine different evolutionary trends among mimosoids. A comprehensive understanding of differing order of organogeny of sepals and stamens should help to define the tribes and establish how differences among them have arisen. The difference between positions of organs may represent a significant discontinuity which requires

assessment of relationships to the other subfamilies. Comparative development will greatly help in determining polarity of character states. New character states may be determined to broaden the array of systematic criteria at different levels. Convergence, parallel evolution, and neoteny will likely become evident if present, through comparison of ontogenies.

Developmental details of inflorescence architecture and floral organogeny is presented for one representative genus of the simplest tribe Mimoseae in Chapter 2. This chapter represents the type of analysis done for each of the 39 species studied. Order of organ initiation for particular parts of floral ontogeny is analyzed and discussed in Chapter 3 and Chapter 4. Comparative sepal initiation in 39 species is covered in Chapter 3. Comparison of divergent pattern of stamen initiation and proliferation in 22 species is presented in Chapter 4. A literature review relevant to the research is presented in Chapter 1.

Floral ontogenetic study in mimosoids presumably is significant because is an innovative approach to mimosoid systematics with potential to determine polarity of character states and evolution of the group.

Literature Review

Chapter 1

Mimosoideae: General description -- Mimosoideae is the smallest of the three subfamilies of legumes (Bentham, 1875; Cronquist, 1968; Chant, 1985) with representatives distributed mostly in the tropics and subtropics. Generally it is distinguished from the other two subfamilies (Caesalpinioideae and Papilionoideae) by its bipinnate leaves, actinomorphic flowers, valvate aestivation, and 10 or more stamens per flower.

Originally, six tribes were described within the group (Bentham, 1875; Taubert, 1891-1892; Schulze-Menz, 1964; Hutchinson, 1964). Recently, five tribes have been recognized based on floral and pollen morphology (Elias, 1981a). The three largest tribes are Mimoseae, Acacieae and Ingeae. Mimoseae has been considered the extant base group with Acacieae and Ingeae more specialized and derived (Elias, 1981a). Parkieae is derived but less specialized; Mimozygantheae is monotypic and presumably derived (Elias, 1981b, c).

Tribal criteria -- The significance of evolutionary trends within tribes of Mimosoideae and the relationships of the subfamily in taxonomy and evolution are summarized by Elias (1981a). Revision of classification among tribes requires more research in determining distribution and sources of variation at different taxon levels (Elias, 1981a, b, c; Lewis & Elias, 1981; Vassal, 1981; Nielsen, 1981). Recent data that enhance systematic knowledge in the subfamily include studies in cytology (chromosome counts) (Goldblatt, 1981), chemistry (Romeo, 1986; Smolenski & Kinghorn, 1981) fruit and seed morphology (Gunn, 1984; Manning & van Staden, 1987; Pries de Lima, 1985) and pollen

morphology (Guinet, 1981).

Mimoseae contains 36 or 37 genera and about 650-725 species (Turner, 1959; Lewis & Elias, 1981). It is characterized by having exserted stamens in one or two whorls, as many as or twice as many as the petals, and filaments free or connate at the base. Lewis & Elias (1981) indicate that generic relationships within the tribe are unclear partially because floral structures in many genera have not been investigated in detail. Information pertaining to differences in adnation and specialization of floral parts is of prime importance. Some taxonomical work is ongoing recently with the discovery of new species in Mimosa (Barneby & Fortunato, 1987) and Desmanthus (Contreras-Jiménez, 1986).

The tribe Acacieae is monogeneric with approximately 2,000 species (Vassal, 1981) on several continents. Flowers are characterized by having numerous stamens in whorls, free or partially fused. A revision of the genus has been recently suggested by Nielsen (1985). Ancibor (1969) determined floral nectary data to have taxonomic significance within the genus. Comparative floral and inflorescence morphology in South African species were studied by Robbertse (1974). The possibility of the origin of the involucel as a new taxonomic criterion for the Gummnifereae species of Acacia was discussed. Buttrose et al. (1981) reported anatomical studies in reproductive floral structures for Acacia pycnantha.

Members of Ingeae are characterized by having numerous stamens and a staminal tube formed by fused filaments. It is perhaps the least

studied tribe in the subfamily; it is tropical and subtropical in distribution (Nielsen, 1981). It contains 17 genera with 950-1,000 species. Delimitiation of genera such as Albizia and Pithecellobium is controversial. Studies on floral biology and phenology in Inga demonstrated mechanisms in pollination based on morphological features in flowers and inflorescences (Koptur, 1983). The new genus Zapoteca, segregated from Calliandra, has recently been proposed (Hernandez, 1987). Description of the new genus was based on palynological characters, seedling morphology, chromosome numbers, inflorescence structure and reproductive features.

Ontogenetic work -- Previous classical morphological work such as that of Payer (1857), Eichler (1878) and Baillon (1872) provides a basis for ontogenetic analysis within mimosoids. The importance of morphology in systematics has been stressed by Davis & Gilmartin (1985) who pointed out the need to determine which characters are more labile than others.

Recent critical developmental work in mimosoids shows that comparative ontogeny of flowers provides new characters (i.e. position of organs) and new character states (i.e. in order of sepal initiation) (Ramirez-Domenech & Tucker, 1988; submitted). Previous work by others reported order of calyx initiation as helical for two Acacia species (Newman, 1936), simultaneous in Calliandra (Tucker, 1984) and Neptunia (Tucker, 1988) and not determinable in Albizia (Sattler, 1973). Stamen initiation, particularly in multistaminate flowers, was discussed by Gemmeke (1982).

The work of Newman (1936) is useful in comparing floral histogenesis in two multistaminate Acacia species, differing greatly in histogenesis and in stamen number. Rohrbach (1870) and Hirmer (1916) provide limited but useful information on floral organ initiation among different genera within the three subfamilies and development of multistaminate androecium, respectively.

Inflorescence ontogeny in mimosoids has been dealt by Tucker (1988) in Neptunia pubescens and Ramirez-Domenech & Tucker (in press) in Mimosa strigillosa. Heteromorphy occurs in Neptunia resulting from suppression of lower, first initiated flowers, which become sterile. In Mimosa strigillosa suppression occurs in basal flowers but does not lead to heteromorphism.

More information on developmental characters in mimosoids is summarized in a broad recapitulation of data for the three legume subfamilies (Tucker, 1987).

Ontogeny can play a major role in phylogenetic assessments of taxa among organisms although it has been little used. Good examples include Kirchoff's work (1988) for plants and Kraus (1988) for animals. Crisci & Stuessy (1980) noted that information on developmental patterns may be useful to further understand phylogeny, because phylogenetic changes may arise by modification of ontogeny. Gould (1977) points out that ontogenetic events such as heterochrony, paedomorphosis, progenesis and neoteny, may be significant to determine phylogeny in several taxa among animals. In plants, ontogenetic studies in vegetative parts are rather inconclusive as to phylogenetic significance

because growth is indeterminate. However, in flowers growth is determinate, so that complete sequences of ontogenies can be compared. Cladistic work using ontogenetic data is pursuit but is not at the stage for discussion (Ramírez-Domenech & Tucker, personal data).

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Phylogenetic Implications of Inflorescence and Floral Ontogeny of *Mimosa strigillosa*

Chapter 2

INTRODUCTION -- Although most mimosoid species have flowers which are consistently 3-, 4-, or 5-merous and radially symmetrical, some species, such as Mimosa strigillosa Torr. & Gray, regularly vary in number of parts and in pattern of organ arrangement. Species in the genus Mimosa regularly vary in number of parts (tetramerous in some species, pentamerous in others) and in diversity of organ arrangement, more so than other mimosoids studied. Mimosa is a widespread genus in tropical and subtropical areas, with the majority of species represented in the New World and few species in the Old World (Isely, 1971; Lewis & Elias, 1981). In spite of that, developmental studies are few. Floral development information on the genus has been limited to the common weedy species, Mimosa pudica L. (Baillon, 1872; Eichler, 1878; Gemmeke, 1982; Tucker, 1984). The present work is part of a more comprehensive study underway in our laboratory, of comparative floral ontogeny among mimosoids. Ramírez-Domenech & Tucker (1988) have reported data on order of organ initiation and position of organs in 11 species of mimosoids, including three species in Mimosa L. (M. pudica L., M. caesalpinifolia Benth., M. strigillosa).

Mimosa strigillosa is a perennial herb with spineless, prostrate stems, native to southeast USA, Mexico, Paraguay and Argentina (Correll & Johnston, 1970). This species was selected becuase it shows variation in merosity and is representative of the most primitive tribe, Mimoseae. Floral ontogeny of representative genera of the more derived tribes are planned for later.

Intraspecific variation in the number of parts, pattern of organ

arrangement, and developmental pathways of inflorescence architecture are important aspects that needs further investigation among mimosoids. Mimosa strigillosa is unusual among mimosoids investigated in that there are two patterns of organ position in the same inflorescence. These patterns are described below. The inflorescence of Mimosa strigillosa exhibits temporary suppression of organogeny in some flowers of the inflorescence. The relationship between suppression and heteromorphy of flowers will be explored.

MATERIALS AND METHODS -- Study material of Mimosa strigillosa was collected during two growing seasons from a population in Baton Rouge, Louisiana. Other collections were obtained from Cancún, Mexico; Mayagüez, Puerto Rico; and Miami, Florida. Vouchers are deposited at LSU. Most work was done on the Baton Rouge collections. The material was preserved in FAA (formalin-acetic acid-alcohol). Flower buds were dehydrated to 95% alcohol and dissected. They were further dehydrated and critical point dried, mounted on stubs with graphite and coated with gold-palladium in a Hummer II sputter coater. The material was studied with a Hitachi S-500 scanning electron microscope (SEM) at 25 kv, and micrographs taken on Kodak Tri-X-Ortho film.

RESULTS -- Development will be described and illustrated for the population of M. strigillosa from Louisiana; additional material from Mexico and Puerto Rico has similar ontogeny.

Inflorescence -- Inflorescences of M. strigillosa appear globose and umbellate (Fig. 1), one in each leaf axil on prostrate leafy branches. They actually are racemes as will be shown later. Each

leafy branch is indeterminate, having succession of progressively younger inflorescences toward the tip. In other words, one shoot may have many stages, including fruits (Fig. 2), each at a different node. At anthesis, the inflorescence axis is ca. 2 cm long and the peduncle ca. 5 cm long. There are from 90-100 flowers arranged along approximately 7 spiral parastichies. In young inflorescences the subterminal flowers are so tightly packed that each inflorescence seems to have a terminal flower (Figs. 6, 8).

During early development each inflorescence apex is convex and transversely circular, and is unusually initiated on the flank in axillary position immediately below the vegetative apex (Fig. 3). The bract primordia are formed by the inflorescence apex in acropetal succession and helically along the inflorescence axis (Fig. 5) starting above a short peduncle (Fig. 4). At the stage shown in Figure 5 the inflorescence axis can be distinguished from the peduncle by the presence of early bract primordia. Bract formation ceases when the inflorescence apex terminates in an apical residuum (Fig. 7). The last organ formed is approximately 803 μm long at this time.

In the inflorescence, flower buds are located singly in the axil of each subtending bract (Figs. 7, 8), and bracts are crowded and overlapping (Fig. 10). Most flowers develop synchronously in any one inflorescence during organ initiation (Figs. 6, 8, 10). Flowers in the upper and middle regions along the inflorescence axis share the same stage of organogenesis (Figs. 8, 10). The exceptions are the basal flowers which are suppressed early and undergo organogenesis

later than the flowers above (Fig. 11), although their development is the same as in the upper flowers.

Organography -- Flowers are perfect (Fig. 37) and actinomorphic (Fig. 40). The petals and filaments are pink, and the anthers are yellow. Generally flowers are tetramerous (Fig. 40), with occasional pentamerous flowers (Figs. 38, 41) in the middle and lower regions of the inflorescence. The calyx is minute (at arrow, Fig. 43), tubular (Fig. 42), irregular lobate (Figs. 40, 41) and has hairs at its rim (Figs. 38-43). The corolla is fused over half its length with free lobes appressed in bud (Fig. 43). The androecium is diplostemonous, with 8 (10) free stamens in two whorls: an outer (antesepalous) whorl and an inner (antepetalous) whorl (Fig. 27). At anthesis, stamens are long exserted (Fig. 44) and each tetralocular anther (Fig. 34) is dorsifixed (Fig. 35), subtended by a distally tapered filament (Fig. 45). The carpel is terminal with an adaxial cleft (Fig. 32). At anthesis the ovary is sessile and villous throughout (Fig. 47). The style is straight, elongate (Fig. 44) with a tapered stigma (Fig. 46).

Organogenesis -- A bare flower meristem arises in the bract axil (Fig. 12) and is rounded, transversely circular in shape and about 59 μm in diameter. The meristem then flattens as it widens up to 70 μm (Fig. 13). The calyx arises as a ring meristem (Fig. 14) which will form a calyx cup (Fig. 15). The tube elongates evenly or erratically (Figs. 16, 17, 18). Generally the adaxial side grows faster than the abaxial side and sometimes overarches the center (Figs. 25, 41). The calyx remains tubular and short through anthesis (Fig. 42)

and never encloses the flower. A few minute hairs form at the rim of the calyx tube (Fig. 39).

Petals next arise simultaneously, equidistant, equal sized, and free. The floral meristem, after petal initiation, is approximately 87 μm wide, in four-merous flowers (Fig. 19) and about 100 μm in five-merous flowers. In five-merous flowers, the petals are not equidistant; two of the more adaxial petals arise close together (Figs. 22, 47D, E) and appear smaller than the rest.

Determination of the pattern of symmetry is based on the alignment of petals in relation to the subtending bract. We use petal position rather than that of sepals in Mimosa, because sepals are fused at initiation, and they enlarge erratically. Flower symmetry can be in either of two patterns, both found in four-merous and in five-merous flowers. Pattern 1 (median sagittal pattern, Fig. 48C) has two median sagittal petals and two laterals (Fig. 21). Pattern 2 (non-sagittal pattern, Fig. 48B) has two abaxial and two adaxial petals (Fig. 20). In pentamerous flowers, the median sagittal pattern contains a median sagittal petal abaxially, a pair adaxially, and two laterals (Figs. 23, 48E) and the non-sagittal pattern has a median sagittal petal adaxially (Figs. 22, 48D).

Development of the petals is characterized by synchronous enlargement (Fig. 24), beginning when the calyx tube is approximately 60 μm high. At the pre-stamen stage (Fig. 20) the meristem is about 92 μm wide and the petals are about 63 μm wide at the base and approximately 21 μm long. When the petals are about 51 μm long they

start to curve inward (Fig. 25). At this stage the first whorl of stamens and the carpel have already initiated. The remainder of the meristem will be utilized by initiation of the second whorl of stamens (Fig. 26). The petals meet when the calyx tube is about 106 μm long (Fig. 42) and enclose the inner parts of the flower bud in valvate aestivation (Fig. 39).

Four stamens are initiated simultaneously, equidistant and equal in size in each of two alternate whorls. An antesepalous whorl arises first (Fig. 24) when the floral apex is about 75 μm wide. The antepetalous whorl arises later (Fig. 26), after carpel initiation. The floral meristem is used up after this stage. The antepetalous whorl of stamens has enlarged by the time the carpel is about 50 μm and the antesepalous stamens about 30 μm long (Fig. 27). In a median sagittal pattern in four-merous flowers members of the outer whorl of stamens are all lateral: two adaxial and two abaxial (Fig. 32), and in a non-sagittal pattern two of the stamens of the outer whorl are in the median sagittal plane and two are lateral (Fig. 24). Only one pattern is illustrated for stamens in five-merous flowers (Fig. 23), which each have a median sagittal stamen adaxially. The antesepalous stamens start to widen distally when they are about 79 μm long (Fig. 29) and first show form differentiation as anthers and filaments when the stamen is about 143 μm long (Fig. 31). As early as the stage shown in Figure 27 the two whorls of stamens are reoriented into a single whorl, a haplostemonous condition. The anthers in outer stamens (antesepalous) cover the inner stamens (antepetalous) whorl,

while the anthers in antesepalous stamens widen distally, when the stamens are approximately 172 μm long and the filaments are about 128 μm long (Fig. 33).

During elongation the corolla tube encloses the stamens in bud and the filaments elongate and become folded (Figs. 35, 36). The stamens are long-exserted at flower opening (Fig. 44), and the anther is dorsifixed subtended by a distally tapered filament (Fig. 45).

The carpel is terminal and arises as a central circular mound (Fig. 25) before the antesepalous whorl of stamens are initiated. It enlarges to form a high-convex dome (Figs. 27-28) and forms an adaxial cleft when about 46 μm high (Fig. 28). The antesepalous stamens are about 34 μm long at this time. The carpel remains open before stamen form differentiation begins (Fig. 30). At the stage in Figure 32, the carpel margins are appressed. The filamentous style is folded distally in bud (Fig. 37) and becomes exserted and much elongated at anthesis (Fig. 44).

DISCUSSION -- Influence of suppression in inflorescences -- The onset of organogeny of the lower flowers of inflorescences is retarded or temporarily suppressed in M. strigillosa, as in several other mimosoid genera (Tucker, 1987). Comparisons among inflorescences at different developmental stages have shown that although flowers are initiated in acropetal order they develop synchronously except for the basal flowers which are retarded. In this case we refer to suppression as the condition where organogeny is delayed. Consequently, floral organogeny is not synchronous among all flowers in an

inflorescences.

Developmentally there seems to be a correlation between heteromorphism and basal flower suppression, in about five heteromorphic species studied. But in M. strigillosa the connection breaks down; suppression occurs but not heteromorphy. In heteromorphic genera such as Neptunia it has been observed that suppressed flowers differ morphologically and functionally in inflorescences, while in M. strigillosa there are no morphological distinctions among flowers. Suppression here does not lead to heteromorphy. Other examples of heteromorphic inflorescences in mimosoids are found in Dichrostachys, Parkia (Baillon, 1872), Neptunia lutea (Windler, 1966), Albizia, Samanea and Desmanthus (unpublished observations). Inflorescences of several other taxa of mimosoids are being studied developmentally in order to determine the role of suppression in heteromorphy.

The possibility that suppression operates here to build up a system for optimal seed and fruit production has been considered. After pollination in M. strigillosa, fruits develop only in the upper and middle regions of the inflorescence and are absent at the base (Fig. 2). The total number of fruits is always less than the total number of flowers (See Figs. 1, 2). A functional concept applied to explain heteromorphism, seems to apply as well to explain suppression. Elias (1981) suggested the concept of 'division of labor' to explain heteromorphism. He proposed that energy in inflorescences may be canalized in such a way that would allow for the establishment of defense systems, or optimal fruit or seed production. We suspect that

in M. strigillosa suppression is an adaptation to help guarantee an optimal production of seed and fruit.

Calyx -- A ring-like calyx initiation can be interpreted as precocious fusion of separate primordia. The ring meristem is a distinctive feature of Mimosa, as has been shown in M. strigillosa, M. pudica (Gemmeke, 1982; Tucker, 1984), M. albida and M. pigra (unpublished data). In most mimosoids the sepals arise separately and in helical order although additional patterns have been found (Ramirez-Domenech & Tucker, 1988). Precocious calyx fusion may be considered an advanced condition for the tribe and probably is specialized within the genus. According to the concept of increasing precocity of gene action (Stebbins, 1974) precocity of appearance of a derived characteristic (like fusion) is advanced phylogenetically.

The calyx tube does not enclose the petals at any stage in bud in either M. strigillosa or M. pudica (Tucker, 1984). Polhill et al. (1981) said that the occurrence of this feature in the Dimorphandra group in Caesalpinioideae, is evidence for its presumed transitional relationship to mimosoids. We have found this feature in 38 other species of mimosoids studied.

Excessive adaxial growth in the calyx cup of M. strigillosa to produce a hooded appearance is considered a tendency toward zygomorphy in a group (mimosoids) where zygomorphy is rare. Adaxial parts of the calyx cup elongate to varying extents, and partially overarch the bud while the abaxial side may elongate later in ontogeny. A similar condition was also observed for M. pudica (Tucker, 1984). Eichler

(1878) described the tribe Mimoseae as exhibiting weak zygomorphy in the calyx. Zygomorphy also has been observed in male flowers of Neptunia pubescens late in development (Tucker, 1988). The zygomorphy in M. strigillosa in the calyx is variable and is expressed late in ontogeny, suggesting that it is a relatively labile feature. The genetic potential for zygomorphy is present but rare, and expressed late and/or weakly in mimosoids, whereas zygomorphy is the rule in the other two subfamilies of legumes. In papilionoids, zygomorphy is initiated precociously in the calyx whorl, while in most caesalpinioids it is not expressed until petal initiation (Tucker, 1984; Tucker et al. 1985). Mimosoids would then be considered the least specialized of the three, in regard to the zygomorphy character.

Merosity -- The number of parts per whorl has been suggested to be an early-determined feature in legumes (Tucker, 1984). Most legumes are characterized by a basic pentamerous floral architecture (Fig. 47A). Species of Mimosa, can be tri-, four-, or five-merous. Several species of Mimosa are known to have a variable merosity among flowers within an inflorescence (Schulze-Menz, 1964). Mimosa strigillosa is four-merous with occasional five-merous in the same inflorescence.

Variability in number of floral organs in mimosoids may be achieved through reduction or increase. Reduction in the number of organs as well as loss of an entire whorl is common among legumes, particularly in caesalpinioids (Tucker et al. 1985; Tucker, 1987). Among families other than legumes, higher numbers are considered primitive, and decreased numbers derived. Loss due to fusion or suppression has been

thought responsible for different number of parts in floral whorls in Mitchella repens (Blaser, 1954), members of the Polygonaceae (Laubengayer, 1937) and reduction in sepal number in Aegle marmelos (Rutaceae) (Leins, 1967). In primitive angiosperms, a decrease in organ numbers has been associated with fusion of parts and a tendency toward whorled initiation (Endress, 1987). Other reports among angiosperms, specifically in Onagraceae, have suggested the four-merous condition to be primitive and pentamery is advanced (Eyde, 1977).

We have applied Eichler's (1878) interpretation of the calyx in M. pudica to analyze the possible ways in which a four-merous corolla may have been established in M. strigillosa and M. pudica. Eichler (1878) suggested that the four-merous condition in the calyx in Mimosa was derived from a basically five-merous flower. Eichler compared Plantago and other 'pseudotetramerous' flowers in the Labiatae to M. pudica to indicate that the four-merous condition may have been achieved in various ways, such as: suppression of an adaxial organ, fusion of the adaxial organ to an adjacent lateral organ through a process that Eichler called "prosenthese" or "removal". We suspect that in M. strigillosa, fusion between two adjacent petals may have occured to produce a four-merous condition in some flowers. Reduction in meristem size may result in fusion of two adjacent petals or initiation of fewer petals due to lack of space. Tucker (1960) and Stebbins (1967) proposed that the size of the meristem at a particular stage of development is one factor that controls the number of parts which can be produced. Other explanations for variability in the number of parts among

angiosperm flowers include adaptations to coevolutionary forces in the environment (Leppik, 1956) or genetic plasticity (Huether, 1968).

Variable organ arrangement -- Mimosa strigillosa appears to be unusual among other mimosoids studied in that two patterns of petal arrangement commonly occur (Figs. 48B, C). According to Eichler, the common or basic four-merous pattern for mimosoids is one with two sepals in the median sagittal plane and two lateral sepals. The petals are located in non-sagittal planes, two adaxial and two abaxial (Fig. 48B). Eichler described an unusual pattern in M. pudica with sepals arranged in a non-sagittal plane and two of the petals in a median sagittal plane (Fig. 48C). Each inflorescence of M. pudica shows only one pattern (Eichler, 1878; personal observation). Mimosa strigillosa contains flowers with either a median sagittal (Fig. 48C) or a non-sagittal pattern of petal arrangement (Fig. 48B). Since non-sagittal is the most common in the subfamily (personal observations) I suspect that the median sagittal pattern may have been derived from the non-sagittal pattern.

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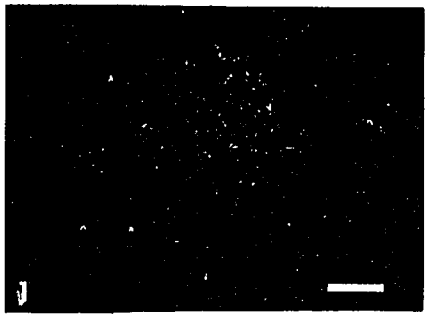
Figs. 1-2. Inflorescences of M. strigillosa at anthesis and in fruit. 1. Flowers in inflroescence raceme at anthesis. 2. Fruits present in upper and middle regions. Arrow points to flower scars and bracts at the base of inflorescence. Bar = 1 cm.



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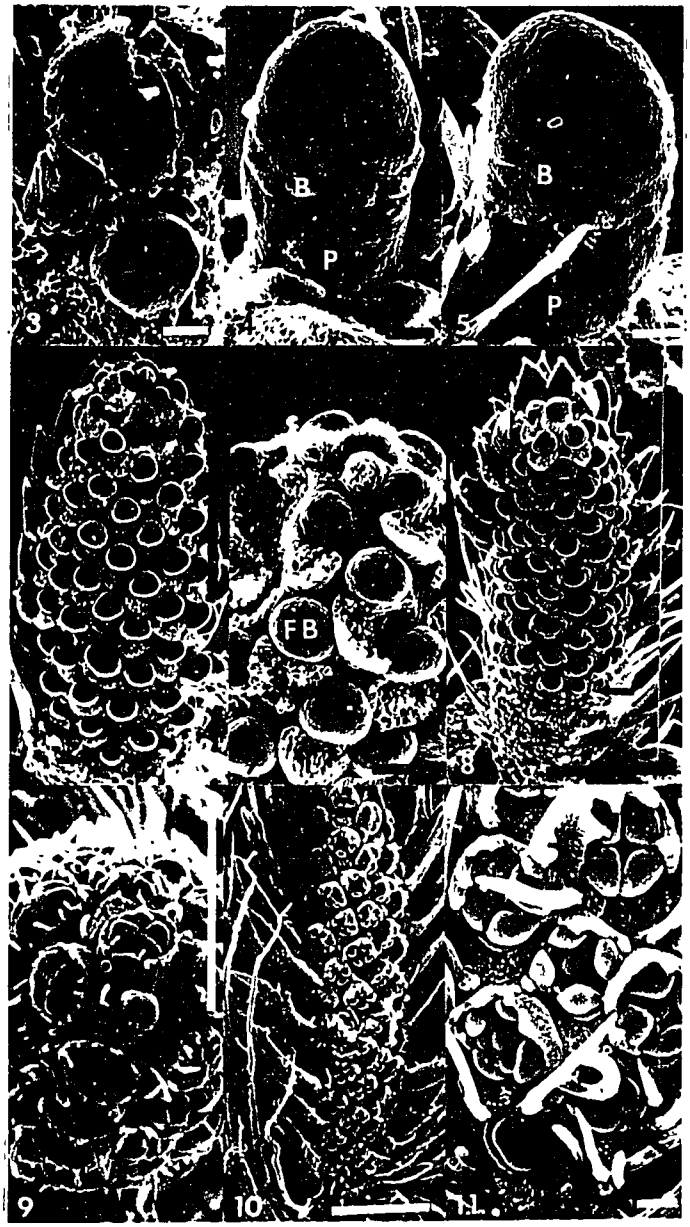
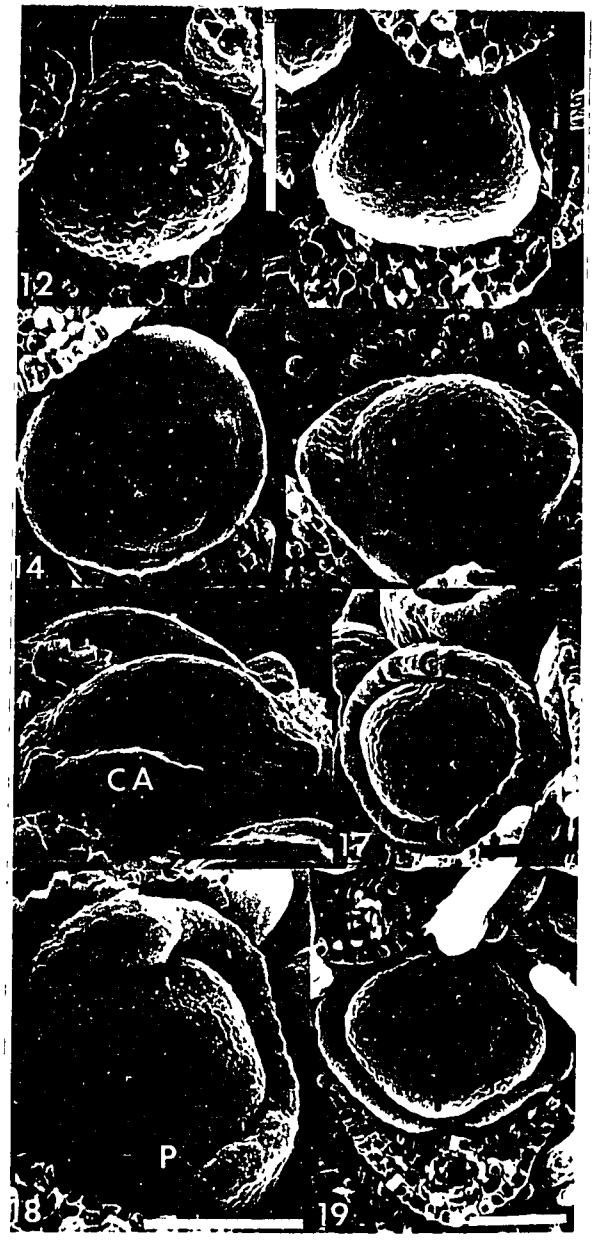
Figs. 3-11. Inflorescences of M. strigillosa at various stages of development (SEM preparations). Bracts have been removed in all except 4, 5. 3. Inflorescence apex, in axil of bract, is marked with a star. Vegetative apex and early leaves shown at arrow. 4-5. Early inflorescence meristems undergoing bract formation. Apices are marked with stars. 6. Inflorescence after initiation of flower primordia in bract axils. All floral apices are at the same stage (no organs). Basal flower primordia (at arrow) are smaller than the rest. 7. High magnification of inflorescence in Fig. 6 to show apical residuum (at arrow). 8. Inflorescence during calyx initiation. Arrow points to suppressed floral primordia. 9. Near-polar view of older inflorescence. 10. Side view of inflorescence after organ initiation is complete in flowers. 11. Flowers at several stages near base, with suppressed flowers (at arrow) in basal region. B, bract; FB, flower bud; P, peduncle. Bar = 50 μm, except in Figs. 8, 9, 10, where bar = 500 μm.


B
P
B
P
FB

Figs. 12-19. Floral buds during early organogenesis (SEM preparations). Subtending bract has been removed in all. Abaxial side is at base in all except Fig. 15, 16. 12. Polar view of bare flower meristem. 13. Pre-sepal initiation stage. 14-16. Early calyx cup formation (polar, oblique and side views). Calyx ring at arrow. Lobes on the calyx do not correspond to sepal positions. 17. Flower bud with calyx ring during early elongation of the calyx to form a tube. 18. Flower bud with erratic growth in the calyx rim and initiation of four petals (one labelled). 19. Flower bud with bilobed calyx cup and four petal primordia (one labelled). B, bract; CA, calyx; FA, floral apex; P, petal. Bar = 50 μm.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CA
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Figs. 20- 28. Flowers during organogeny of petals, stamens and carpel (SEM preparations). Bract has been removed in all. Abaxial side is at base in all. Figs. 20-21. Polar views of four-merous flowers showing contrasting patterns of petal arrangement. 20. The non-sagittal pattern consisting of two lateral petals in abaxial position and two lateral petals in adaxial position. 21. The median sagittal pattern consist of two median petals and two lateral petals. 22-23. Polar views of five-merous flowers showing patterns of petal arrangement. The non-sagittal pattern consist of a median sagittal petal adaxially, two laterals, and two abaxially (Fig. 22). The median sagittal sagittal pattern consist of a median sagittal petal abaxially, two petals adaxially and two laterals (Fig. 23). 24-25. Four-merous flowers showing early enlargement of petals. 24. Initiation of carpel primordium (at big arrow) and the whorl of antesepalous stamens (at small arrows). Line bisects the flower through its plane of symmetry. 25. Pre-stamen stage. The calyx grows faster in the adaxial side and tend to overarch the center of the flower bud. 26. Polar view of initiation of antesepalous stamens (at arrows). Carpel has become a convex mound at center. 27. The antesepalous stamens are approximately 23 um high. Both carpel and antesepalous stamens are dome-shaped. 28. Flower with incipient carpel cleft adaxially. The antesepalous stamen (at arrow) has become convex in shape. Only one stamen per whorl is labelled (antesepalous and antepetalous). AS, antesepalous stamens; AP, antepetalous stamens; B, bract; C, calyx; G, carpel; P, petal. Bar = 50 μm.


21
21
22
P
P
S
S
P
S
P
S
S
P
B
23
S
S
G
S
S
26
AS
AS
G
AS
AS
27
AP
AS
G
28

Figs. 29-37. Flowers showing stamen organogenesis and development of the androecium and carpel (SEM preparations). The calyx and corolla have been removed in all, except in Figs. 35-37. 29-30. Side and polar views of flower at stage when antesepalous stamens (about 79 um long) are beginning to widen distally. Antepetalous stamens are about 51 um high. 31. Anther and filament are identifiable in outer stamen. 32. Early closure of carpel cleft (polar view). 33-35. Anther differentiation. 33. Side view of flower bud showing relative length of antesepalous stamens (172 um) when the anthers start to show locules. Polar view of flower to show tetralocular anthers before anthesis. 35. Side view of flower bud with dorsifixed stamens. 36-37. Mature buds with folded stamen filaments inside lightly fused petals (36) and terminal carpel (37). Petals have short interlocking hairs on the inner surface and margins (at small arrows). AS, antesepalous stamens; AP, antepetalous stamens; B, bract; G, carpel; P, petals; S, stamens. Bar = 50 μm except in Figs. 35-37, where bar = 500 μm.


G
AS
AP
29
30
S
S
S
31
S
S
S
32
S
S
34
P
S
G
35
P
S
F
36

Figs. 38-43. Mid to late stages of flowers showing short calyx tube, and valvate corolla (SEM preparations). Subtending bract has been removed in all, except in Fig. 43 where the bract remains subjacent to the flower. Abaxial side is at base in all except in Fig. 43 where is toward the right side. 38. Adjacent four-merous and five-merous. One petal is subequal in lower flower. 39. Polar view of a four-merous flower showing valvate aestivation. The calyx tube never encloses the flower in bud. 40. Polar view of flower during corolla closure showing equal-sized petals. The calyx exhibits excessive growth adaxially. The rim of the calyx is deeply lobed. 41. Five-merous flower during corolla closure showing unequal sized petals. 42. Calyx tube and corolla lobes (side view). The calyx tube does not show lobes on the rim at this stage. 43. Flower bud with short calyx tube (at arrow) and subtending bract. Note long corolla tube. Hairs are present in petal lobes above the fusion. B, bract; C, calyx; ST, calyx tube; CT, corolla tube; P, petal. Bar = 50 μm in all except inFig. 43 where bar = 500 μm.


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Figs. 44-47. Flowers after opening (SEM preparations). 44. Flower with exserted stamens and style and tubular corolla; calyx at base. 45. Dorsifixed anther and filament and tapered filament (at arrow). 46. Narrow porate stigma (pore at arro). 47. Ovary of flower at anthesis. Calyx, corolla and part of the androecium have been removed. Bar = 500 μm.


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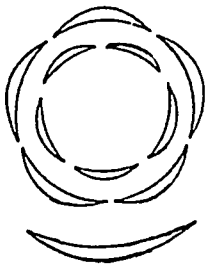
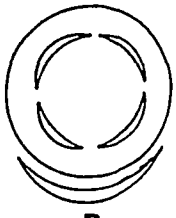
Fig. 48. Diagram of patterns of arrangement in four- and five-merous flowers in the genus Mimosa. A. General five-merous pattern type of flowers in the Subfamily Mimosoideae. B-C. Four-merous flowers with bracts, petals and calyx cup shown. Non-sagittal pattern is shown at (B) and the median sagittal at (C). D-E. Five-merous flowers with bracts, petals and calyx cup. Non-sagittal pattern is shown at (D) and median pattern at (E).



A



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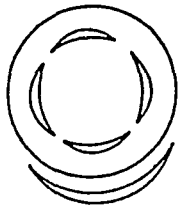

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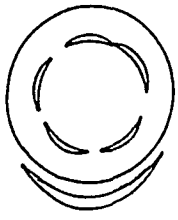

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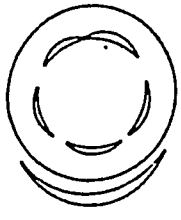

E

Comparative Ontogeny of the Perianth in Mimosoid Legumes

Chapter 3

INTRODUCTION -- Position of organs and order of organ initiation are significant developmental characters which can help to determine evolution of the perianth within the subfamily Mimosoideae. A preliminary report (Ramirez-Domenech & Tucker, 1988) has demonstrated that early calyx initiation varies among different genera and species, and that position of organs is significant at the subfamily level. Previous reports on organ initiation have been documented for several species that include: Acacia Mill. (Rohrbach, 1870; Newman, 1936; Derstine, 1988), Albizia Durazz. (Sattler, 1973), Neptunia Lour. (Tucker, 1988), Mimosa L. (Tucker, 1984; Ramírez-Domenech & Tucker, in press), Calliandra Benth. (Tucker, 1984) and several other genera by Gemmeke (1982), Tucker (1987) and Ramírez-Domenech & Tucker (1988).

Comparative floral ontogeny among the three major tribes (Mimoseae, Acacieae, Ingeae) in the subfamily Mimosoideae has been studied as part of a broader research program by Tucker in floral development in the family Leguminoseae. Early development of the perianth will be discussed in this paper. Four different patterns in order of organ initiation in the calyx will be analyzed developmentally emphasizing four genera representative of the three tribes studied.

MATERIALS AND METHODS -- Inflorescences and flowers of different sizes of representative species were collected and fixed at various locations (See Table 1). Vouchers of specimens are deposited either in the herbarium at LSU or in personal collections. Specimens were fixed in FAA (formalin-acetic acid-alcohol) solution and dehydrated and dissected in 95% alcohol. In order to prepare the material for SEM

(scanning electron microscopy) the following steps were followed: dehydration in an acetone-alcohol series; critical point drying in a DENTON DCP-1 drying apparatus; mounting on stubs with colloidal graphite and coating in a Hummer II sputter coater with gold-palladium. Observations were made using a Hitachi S-500 SEM at 25 kv. Photomicrographs were taken using Kodak Tri-X-Ortho film.

RESULTS -- Flowering material was examined of 18 genera and 39 species in three major tribes of mimosoid legumes. Initiation of the perianth parts occurs in acropetal sequence. The calyx arises in a first whorl followed by a second whorl of petals. Four different types of order of calyx initiation were found during early organogeny: helical, bidirectional, simultaneous and ring meristem. Two types of order of initiation, simultaneous and helical, occur in the corolla. Distribution of order of organ initiation among tribes is represented in Table 2.

Details on development during order of initiation of the calyx will be presented for each of four types found in the following representative species: Mimosa albida, Adenanthera microsperma, Zapoteca portoricensis, Wallaceodendron celebicum.

Ring meristem -- Mimosa albida is native to Central and South America. It is small shrub with pink flowers in racemes located in leaf axils. Flowers are actinomorphic, perfect and tetramerous (Fig. 1a). The calyx is short, tubular, with long, exserted hairs on its rim. The corolla is tubular with four petals fused half their length.

Each flower arises as a bare floral apex in the axil of a bract.

Floral meristems, at the pre-appendage stage, are tansversely broad in shape and about 50 μm in diameter (Fig. 2). Differences in symmetry between calyx and corolla arise during early organogeny. The calyx exhibits slight dorsiventral symmetry and the corolla is radially symmetrical. Initiation of the calyx is characterized by expansion of the meristem forming a ring-like structure, which is approximately 60 um in diameter, slightly concave at the center (Fig. 3). The ring meristem elongates unevenly (Fig. 4) and forms a calyx cup (Fig. 5). The adaxial side grows faster than the abaxial side and curves inward partially overarching the apex (Figs. 6, 7). Lobes along the calyx rim do not correspond to sepal primordia. Sepals cannot be used to indicate symmetry of the flower due to their erratic growth. Symmetry can be determined based on the alignment of petals in relation to the subtending bract.

Petals arise simultaneously and free (Fig. 6). Four separate primordia arise equidistantly in a meristem approximately 70 μm wide. Symmetry is characterized by a median sagittal pattern consisting of two median sagittal petals and two laterals (Fig. 7). Each petal primordium expands initially outward (Fig. 6). They tend to arch over toward the center of the flower at about 50 um high. Petals meet to enclose the bud in valvate aestivation (Fig. 8) when they are approximately 70 μm long. The free margins of the petals become appressed (Fig. 9) and marginal epidermal cells interlock with adjacent epidermal cells at the tips (Fig. 10).

Other species of Mimosa have been found to have a ring meristem

initiation (See Table 2). The only other mimosoid genus in which a ring meristem has been found is Schrankia (Fig. 39).

Simultaneous whorl -- Zapoteca is a genus segregated from Calliandra (Hernandez, 1986). It is represented by 25 species distributed from southwestern USA to northern Mexico and South America.

Zapoteca portoricensis is a shrub with capitate inflorescences, of long white flowers, in axils of leaves. Flowers are perfect, pentamerous and radially symmetrical (Fig. 1b). The calyx consists of five basally connate sepals and the corolla has five long petals united half their length.

A bare flower meristem arises subtended by an axillary bract along an inflorescence axis. Each floral apex is globose and transversely broad in shape, with a diameter of about 80 μm (Fig. 11).

The calyx is initiated in a simultaneous whorl. Five equal-sized sepal primordia arise equidistant and simultaneously, on a floral meristem that is approximately 150 μm wide (Fig. 12). One sepal is in median adaxial position, two are lateral and two are abaxial in relation to the subtending bract (Fig. 13). The vertical plane of symmetry bisects the adaxial median sepal. Each sepal enlarges and arches, when about 150 μm long. It enlarges more rapidly in length than width (Fig. 14). Sepals remain free throughout initiation (Fig. 15). Elongation and marginal growth occur very late. Hairs are initiated at the margins of each sepal when it is about 178 μm long (Fig. 16).

Petals initiate simultaneously in each flower. Five equidistant

petal primordia arise in a meristem that is about 104 μm wide (Fig. 13). The sepals are approximately 73 μm long at this stage. The petals enlarge synchronously (Fig. 15) and arch inward when they are about 50 μm long. They become appressed and meet to enclose the flower in bud in valvate aestivation (Fig. 17). Basal intercalary growth produces a short corolla tube (Fig. 18).

Simultaneous whorl initiation of sepals has been found in some representatives of the tribe Mimoseae: Neptunia pubescens, Neptunia plena, Schrankia microphylla (Fig. 41), and in one member of Ingeae: Zapoteca portoricensis.

Helical order -- The genus Adenanthera is generally distributed in tropical Asia, Africa and tropical America. Adenanthera microsperma is an unarmed tree with flowers in axillary racemes. Flowers are regular, perfect and pentamerous (Fig. 1c). The calyx is valvate and lobate and the corolla consists of free alternating petals.

Bare flower meristems arise in axils of subtending bracts. Each is about 90 μm in diameter, nearly globose and transversely broad in shape (Fig. 19). Initiation of the calyx parts is helical. Five sepals arise usually in a clockwise sequence in relation to the subtending bract. The first sepal arises abaxially but in a non-sagittal position (Figs. 1c, 20), followed by a sepal in median adaxial position. The third sepal is in abaxial non-sagittal position and adjacent to the first (Fig. 21), and the last two sepals are lateral (Fig. 22). The vertical plane of symmetry bisects the median adaxial sepal (Fig. 24). Lateral sepals are usually retarded during elongation (Fig. 22) and

remain smaller throughout development (Fig. 24). Sepals elongate forming a basal calyx tube, with free lobes arcuate to covered the flower bud in imbricate aestivation (Fig. 27). Hairs are usually present on the calyx lobes margins.

Five petals arise simultaneously and equidistant in a meristem that is about 87 μm wide (Fig. 23). The petals enlarge synchronously in a whorl (Fig. 25). When petals are approximately 53 μm long they arch inward toward the floral apex. They cover the flower in bud in valvate aestivation (Fig. 26) when they are approximately 182 um long. The median petal is abaxial (Fig. 25).

Helical initiation is widely distributed among the three major tribes (See Table 2). In the tribe Mimoseae, it was observed in 8 genera and 10 species, in Acacieae in 8 species of Acacia and in Ingeae in 7 genera and 10 species. In helical initiation, there are two main alternatives. In one, in Adenanthera microsperma (Fig. 22) and Lysiloma bahamensis (Fig. 40), the first sepal primordium arises in median abaxial position. In another, in Acacia greggii (Fig. 37) and Acacia berlandieri (Fig. 38), the first sepal primordium arises in median adaxial position.

Bidirectional order -- Wallaceodendron celebicum is a monotypic genus with distribution restricted to parts of Asia and Australia. Flowers are large and pedicellate in terminal racemes. They are perfect and pentamerous (Fig. 1d). The calyx is a short tube and the corolla is tubular, long and exserted.

Flower meristems arises in axil of bracts. At the pre-appendage

stage, the floral apex is elliptical in shape and about 110 μm wide (Fig. 28). Calyx initiation is peculiar in that it arises in a bidirectional fashion. Two lateral sepals arise simultaneously on a meristem that is approximately 150 um wide (Figs. 1d, 29). A median adaxial sepal follows the inception of the lateral sepals and finally two abaxial sepals arise simultaneously (Fig. 30). The first two sepals elongate faster than the rest partially covering the others (Fig. 31). The median sepal is adaxial. Marginal growth of the sepals occurs very early during inception forming a calyx tube with short free lobes. The early calyx tube elongates and the sepal lobes, bearing hairs, meet to cover the flower in bud in valvate aestivation (Fig. 32). During late development the calyx is tightly fused and encloses the flower in bud.

Five petal primordia arise simultaneously and equidistant in a meristem that is about 160 μm wide (Fig. 33). Petals enlarge synchronously (Fig. 34) and start arching over the meristem when they are approximately 130 μm long. Petals meet and enclose the flower bud in valvate aestivation (Fig. 35). When petals are about 220 μm long the free margins are very thick and when appressed interlock with adjacent epidermal cells enclosing the flower (Fig. 36).

The bidirectional order has also been found in two species in Acacieae: Acacia smallii and Acacia pinetorum (Fig. 42).

Comparison of early organogeny and development of the perianth among species studied -- Among mimosoid flowers, order of calyx initiation is variable while that of the corolla is uniform. Several

developmental events such as primordia inception, time of fusion, establishment of symmetry and aestivation are related to order of organ initiation and serve as basis for comparison.

Helical, simultaneous whorl and bidirectional order of initiation are similar during sepal primordia inception, in that individual sepal primordia arise free and equidistant along the flanks of the floral meristem. However, each type become different by changes during mid-development. Each sepal primordium is recognizable throughout development.

Establishment of floral symmetry occurs during early organogeny. Radial symmetry is persistent throughout ontogeny in most species studied. However, in the genera Mimosa and Schrankia in which sepals arise in a ring meristem, sepals grow unevenly, so can not be used to establish floral symmetry. Petals are used instead. Uneven elongation of the calyx in those creates slight dorsiventral symmetry.

Time of fusion of the calyx varies among genera. In Mimosa and Schrankia, the calyx arises as a precocious ring at inception forming a calyx cup. In Adenanthera microsperma and Wallaceodendron celebicum fusion of the calyx occurs during elongation when individual sepals grow marginally, and become appressed with epidermal cells that contact each other and interlock forming a calyx tube. In these cases, at mid-development sepals cover flowers in bud. Zapoteca portoricensis differs in that individual sepal blades remain free.

Aestivation of the calyx in mimosoids is characteristically valvate. However, it varies during elongation of sepals initiated

in a helical and bidirectional order, in which aestivation is imbricate through mid-development stages. Adenanthera microsperma is exceptional in that it remains imbricate throughout development.

Initiation of the corolla is radial at inception and development. The corolla is characterized by inception of free and equidistant primordia on the meristem. It grows to form an exserted tube with free lobes, generally longer than the calyx tube. Pattern of arrangement of the corolla varies among representative species of Mimosa and Schrankia and other mimosoids studied. Four-merous flowers in Mimosa show either a median sagittal pattern (Fig. 1a) or a non-sagittal pattern. Mimosa strigillosa (Ramírez-Domenech & Tucker, in press) shows both patterns mixed in individual inflorescences.

Position of organs in mimosoids flowers is constant among all pentamerous flowers. The median sepal is located in adaxial position and the median petal is abaxial in relation to the subtending bract.

DISCUSSION -- Phylogeny of order of perianth initiation -- Development of the perianth among mimosoid flowers is characterized by 1) differences in order of sepal initiation (See Fig. 42) and 2) uniformity in corolla development. Four different pathways of calyx initiation can be viewed as alternatives or as stages in specialization. A possible phylogenetic hypothesis based on ontogenetic data of alternatives is represented in Fig. 42. These four orders differ in early development and would be expected to continue along different pathways. However, at least two types (simultaneous whorl, ring meristem) are indistinguishable in later stages. Equalization is the

process by which sepals become uniform in size (independent of order of initiation) (See Fig. 42). This process is significant because, where it occurs, it cancels out the divergences that result from variation at calyx initiation among different ontogenies.

The divergences during ontogenies of similar organisms have been considered to be insignificant variations or perturbations during timing of onset within a conserved morphogenetic program (Alberch, 1985). However, our data indicates that these divergences are more than just perturbations. Each divergent line represent a developmental pathway by which a radial symmetry may have arisen in mimosoid legumes. Radial symmetry is determined during early development and correlated with order of organ initiation (Ramírez-Domenech & Tucker, 1988). Variations in order of sepal initiation, all resulting in radial symmetry, suggest that radial symmetry may have evolved through more than one ontogenetic pathway.

Outgroup comparison suggests a base for polarization of some of the four states. Helical is probably the unspecialized order of initiation, while bidirectional, simultaneous whorl and ring meristem are derived conditions. The simultaneous whorl condition is thought more advanced than helical because of outgroup comparison and ontogenetic evidence, since the time interval of initiation events is reduced to zero. The ring meristem type is the most advanced based on ontogenetic evidence since the ring meristem arises from precocious fusion among primordia as they are initiated. Caesalpinioids are used as outgroup for mimosoids based on strong evidence of relatedness

(Polhill et al. 1981) and some degree of shared primitive character states. The flowers of taxa in genera such as Gleditsia and Gymnocladus represent early levels of legume evolution (Dickison, 1981). Order of initiation in all floral organs of several species of Gleditsia has been found to be helical (Tucker, unpublished data).

Evolution and ontogeny of the perianth -- Parallel evolution may have played a major role in evolution of radial symmetry. The evidence obtained in our research shows differences at initiation which, however produce similar morphologies. A character state such as helical order of calyx initiation occurs in parallel in three different tribes, bidirectional and simultaneous whorl in two. Parallelism has been defined as multiple pathways of evolution similarities through similar genetic or epigenetic mechanisms (Fink, 1982). It is widely documented in zoology (Gould, 1977; Rensch, 1959) and less widely in botany, particularly by examples in angiosperm evolution (Cronquist, 1987; Stebbins, 1974). Kirchoff (1988) showed parallelisms in Zingiberales using ontogenetic data in cladistic analysis, as well as some characters from mature plants.

Fink (1982) suggested that ontogeny does not distinguish convergences from parallelisms. His reasoning was that parallelisms are similar in ontogenetic detail and will not allow discrimination between synapomorphies. Our evidence indicates that parallelisms in order of sepal initiation are detectable by direct observation of early stages. Adult form may not reveal the differences because the early differences may be obscured by later development.

Significance of timing of fusion -- Fusion of sepals occurs in all mimosoids studied, but time of fusion varies. The earlier fusion occurs, the greater degree of fusion at anthesis. In helical and bidirectional order of initiation, sepals usually fuse during mid-development. Sepals in flowers with simultaneous order remain free until late in ontogeny. The ring meristem condition can be interpreted as resulting from precocity of the fusion process. The early appearance of fusion in the ring meristem type may be considered an example of evolutionary acceleration, the appearance of a feature at a point earlier in ontogeny (Gould, 1977).

Significance of position of organs -- The positions of sepals and petals are recognized as a distinct taxonomic character which separates the subfamilies. Position is determined during early organogeny and remains constant throughout development. In mimosoid legumes the median sepal is adaxial and the median petal abaxial in relation to the subtending bract. The pattern differs from that of caesalpinioids and papilionoids in which the median sepal is abaxial and the median petal adaxial. This character may separate the three subfamilies into major groups; mimosoids vs. caesalpinioids and papilionoids.

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Table 1. List of genera and species studied.

Species name	Source	Collector and number
Tribe: Mimoseae		
Mimosa albida H. B. ex Willd.	Veracruz, Mexico	Lievens & Gregory 3116
Mimosa pudica L.	Berkeley, California	Ramírez, 2049
Mimosa pigra L.	Tabasco, Mexico	Lievens & Gregory 2322
Mimosa strigillosa Torr. & Gray	Baton Rouge, La.	Ramírez, 1002
Mimosa caesalpinifolia Benth.	Fairchild Trop. Gard. Miami, Fla.	Tucker, 25182
Dichrostachys cinerea (L.) W. & A.	Tucson, Arizona	Gilberson s. n.
Leucaena leucocephala (Lam.) de Wit	Cancun, Mexico	Ramírez, 2022
	Cabo Rojo, P. R.	Ramírez, 1005
Leucaena glauca (L.) Benth.	Cabo Rojo, P. R.	Ramírez, 1003
Adenanthera microsperma Teijsm & Binn.	Fairchild Trop. Gard. Miami, Fla.	Ramírez & Lievens 2025
Neptunia pubescens Benth.	Fairchild Trop. Gard. Miami, Fla.	Tucker, 25492
Neptunia plena (L.) Benth.	Fairchild Trop. Gard. Miami, Fla.	Tucker, 28029

Continuation table 1.

Calpocalyx dinkaglei Harms.	Royal Bot. Gardens Kew, England	Tucker, 24842
Prosopis glandulosa Torr.	Austin, Texas	Simpson, s. n.
Desmanthus illinoensis (Michx.) MacM.	Baton Rouge, La.	Tucker, 25680
Desmanthus virgatus (L.) Willd.	Sinaloa, Mexico	Luckow, 2989
Desmanthus covillei Britton & Rose	Sonora, Mexico	Luckow, 2806
Desmanthus subulatus (L.) Benth.	Sinaloa, Mexico	Luckow, 2980
Schrankia microphylla Dryand.	Fairchild Trop. Gard. Miami, Fla.	Tucker, 26495
Schrankia quadrivalvis (L.) Britt. & Rose	Tabasco, Mexico	Lievens & Gregory 2321
Tribe: Acacieae		
Acacia baileyana F.v.M.	Royal Bot. Gardens Kew, England	Tucker, 24836
Acacia retinoides Schlecht.	Royal Bot. Gardens Kew, England	Tucker, 24699
Acacia smallii Isely	Baton Rouge, La.	Ramírez, 1007

Continuation table 1.

Acacia berlandieri Benth.	Hidalgo County, Tx.	Lievens, 3017
Acacia greggii Gray	Santa Barbara Bot. Gard., California	Tucker, 28786
Acacia hindsii Benth.	Guerrero, Mexico	Lievens & Gregory 3078
Acacia pennatula (Schldl. & Cham.) Benth.	Veracruz, Mexico	Lievens & Gregory 3122
Acacia pinetorum Benth.	Fairchild Trop. Gard. Miami, Fla.	Ramírez & Lievens 2026
Acacia acuifera Benth.	Fairchild Trop. Gard. Miami, Fla.	Tucker, 25191
Tribe: Ingeae		
Albizia polyphylla Fourn.	USPIS, Miami, Fla.	Tucker, 25490
Albizia julibrissin Durazz.	Baton Rouge, La.	Tucker, 25622
Lysiloma bahamensis Benth.	USPIS, Miami, Fla.	Tucker, 25489
	Fairchild Trop. Gard. Miami, Fla.	Ramírez & Lievens 2038
Inga vera Willd.	Veracruz, Mexico	Lievens & Gregory 3089
Pithecellobium dulce Benth.	Royal Bot. Gardens Kew, England	Tucker, 24733

Continuation table 1.

Pithecellobium glaucum (Roxb.) Benth.	Fairchild Trop. Gard. Miami, Fla.	Tucker, 25190
Zapoteca tetragona (Benth.) H. Hernandez	Mo. Bot. Gard. St. Louis, Mo.	Neill s. n.
Zapoteca formosa (Kunth) H. Hernandez	Mo. Bot. Gard. St. Louis, Mo.	Neill s. n.
Zapoteca portoricensis (Jacq.) H. Hernandez	Royal Bot. Gardens Kew, England	Tucker, 24696
Perarchidendron pruinosum Willd.	Queensland, Australia	Armstrong s. n.
Wallaceodendron celebicum Koord.	Fairchild Trop. Gard. Miami, Fla.	Ramírez & Lievens 2048
Samanea saman Merrill	Fairchild Trop. Gard. Miami, Fla.	Ramírez & Lievens 2006

Table 2. Distribution of order of initiation for the calyx and corolla of several genera among three major tribes of mimosoid legumes.

Species name	Vertical order	Transverse order	
		sepals	petals
Tribe: Mimoseae			
Mimosa albida	a	r.m.	s.w.
Mimosa pudica	a	r.m.	s.w.
Mimosa pigra	a	r.m.	s.w.
Mimosa strigillosa	a	r.m.	s.w.
Mimosa caesalpinifolia	a	h	s.w.
Dichrostachys cinerea	a	h	s.w.
Leucaena leucocephala	a	h	s.w.
Leucaena glauca	a	h	s.w.
Adenanthera microsperma	a	h	s.w.
Neptunia pubescens	a	s.w.	s.w.
Neptunia plena	a	s.w.	s.w.
Calpocalyx dinkaglei	a	h	s.w.
Prosopis glandulosa	a	h	s.w.
Desmanthus illinoensis	a	h	s.w.
Desmanthus covillei	a	h	s.w.
Desmanthus virgatus	a	h	s.w.
Desmanthus subulatus	a	h	s.w.
Schrankia microphylla	a	s.w.	s.w.
Schrankia quadrivalvis	a	r.m.	s.w.

Continuation table 2.

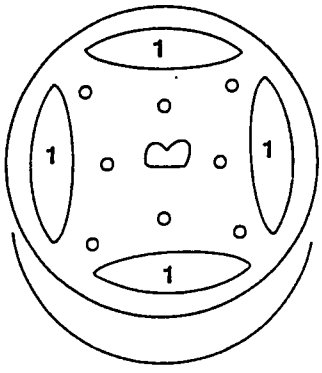
Tribe: Acacieae			
Acacia baileyana	a	h	s.w.
Acacia retinoides	a	h	s.w.
Acacia smallii	a	b	s.w.
Acacia berlandieri	a	h	s.w.
Acacia greggii	a	h	s.w.
Acacia hindsii	a	h	s.w.
Acacia pennatula	a	h	s.w.
Acacia pinetorum	a	b	s.w.
Acacia acuifera	a	h	s.w.
Tribe: Ingeae			
Albizia polyphylla	a	h	s.w.
			h
Albizia julibrissin	a	h	s.w.
Lysiloma bahamensis	a	h	s.w.
Inga vera	a	h	s.w.
Pithecellobium dulce	a	h	s.w.
Pithecellobium glaucum	a	h	s.w.
Zapoteca tetragona	a	h	s.w.
Zapoteca formosa	a	h	s.w.
Zapoteca portoricensis	a	s.w.	s.w.
Perarchidendron pruinosum	a	h	s.w.
Wallaceodendron celebicum	a	b	s.w.

Continuation table 2.

Samanea saman	a	h	s.w.

a; acropetal, b; bidirectional, h; helical, r.m.; ring meristem, sw; simultaneous whorl

Fig. 1. Floral ground plan organization of four mimosoid legumes. Sequence of sepal and petal inception during early organogeny is shown by numbers on each whorl. a) Mimosa albida; b) Zapoteca portoricensis; c) Wallaceodendron celebicum; d) Adenanthera microsperma.



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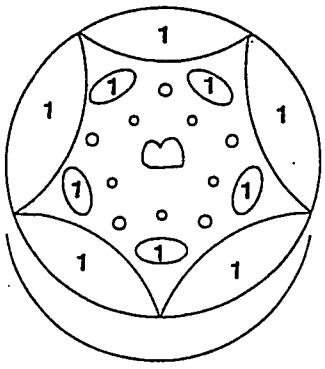

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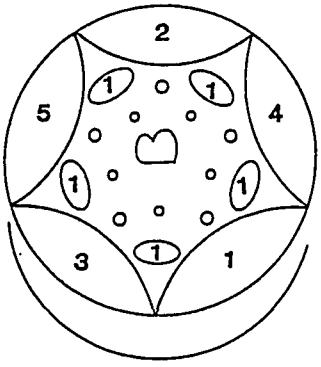

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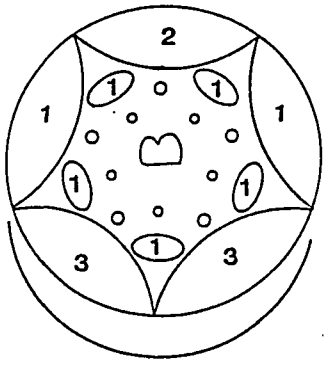

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Figs. 2-10. Flowers of Mimosa albida during early ontogeny and development stages of the perianth (SEM preparations). Subtending bract has been removed in all. Abaxial side at base in all except in Fig. 5. Bar = 50 μm. 2. Polar view of bare flower meristem. 3. Early calyx cup formation. 4. Uneven elongation of the calyx on the adaxial side. 5. Side view of early calyx cup. 6. Polar view of flower with four petal primordia. 7. Flower with uneven enlargement of the calyx and synchronous enlargement of the corolla. 8. Polar view of corolla closure stage. 9. Flower with corolla closed in valvate aestivation. Calyx has been removed. Arrow indicates interlocking hairs. 10. Side view of mature flower. Two petals have been removed. Arrow points to the region of fusion between adjacent petals. B, bract; C, calyx; FA, floral apex; P, petal.


RM
FA
C
B
P
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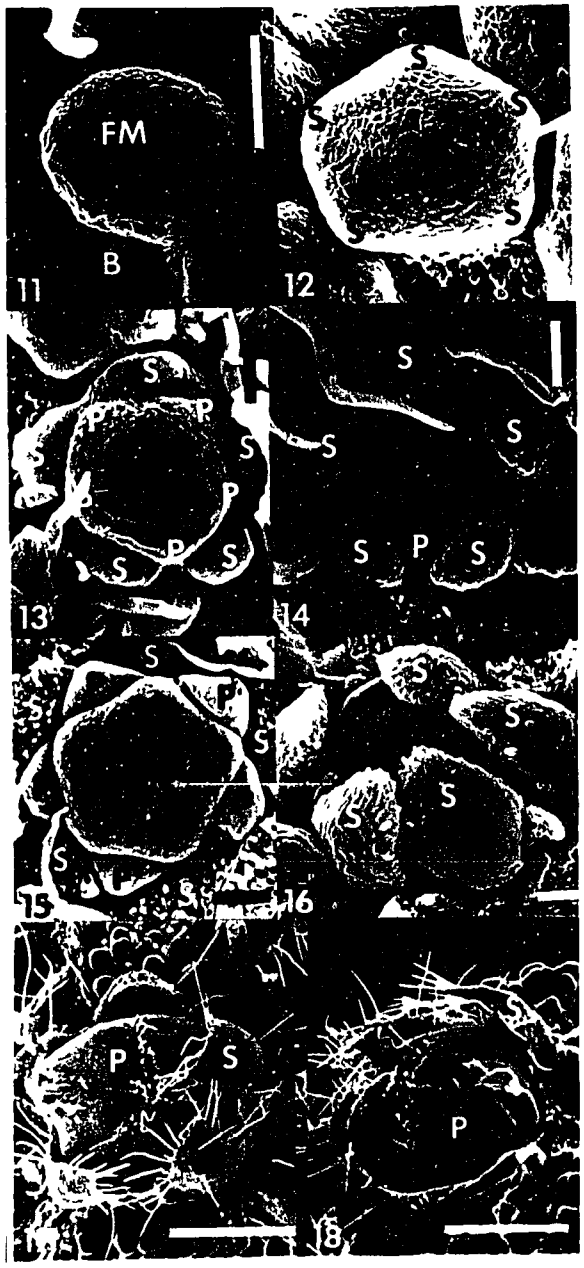
3
4
5
6
10

Figs. 11-18. Young flowers of Zapoteca portoricensis (SEM preparations). Subtending bract has been removed in all. Abaxial side is at base. Bar = 50 μm. 11. Near-polar view of bare flower meristem. 12. Polar view of flower during synchronous inception of sepal primordia. 13. Flower during simultaneous initiation of the corolla. 14. Polar view of flower showing position of sepals and petals in relation to the subtending bract. Median sepal is located and the median petal abaxial. 15. Polar view with synchronous enlargement of petals. 16. Oblique view of flower with sepals arching over the apex. 17. Polar view of flower with petals enclosing the bud in valvate aestivation. Two sepals have been removed. 18. Oblique view of flower bud showing marginal and basal fusion of petals (at arrow). B,bract; P, petal; S, sepal.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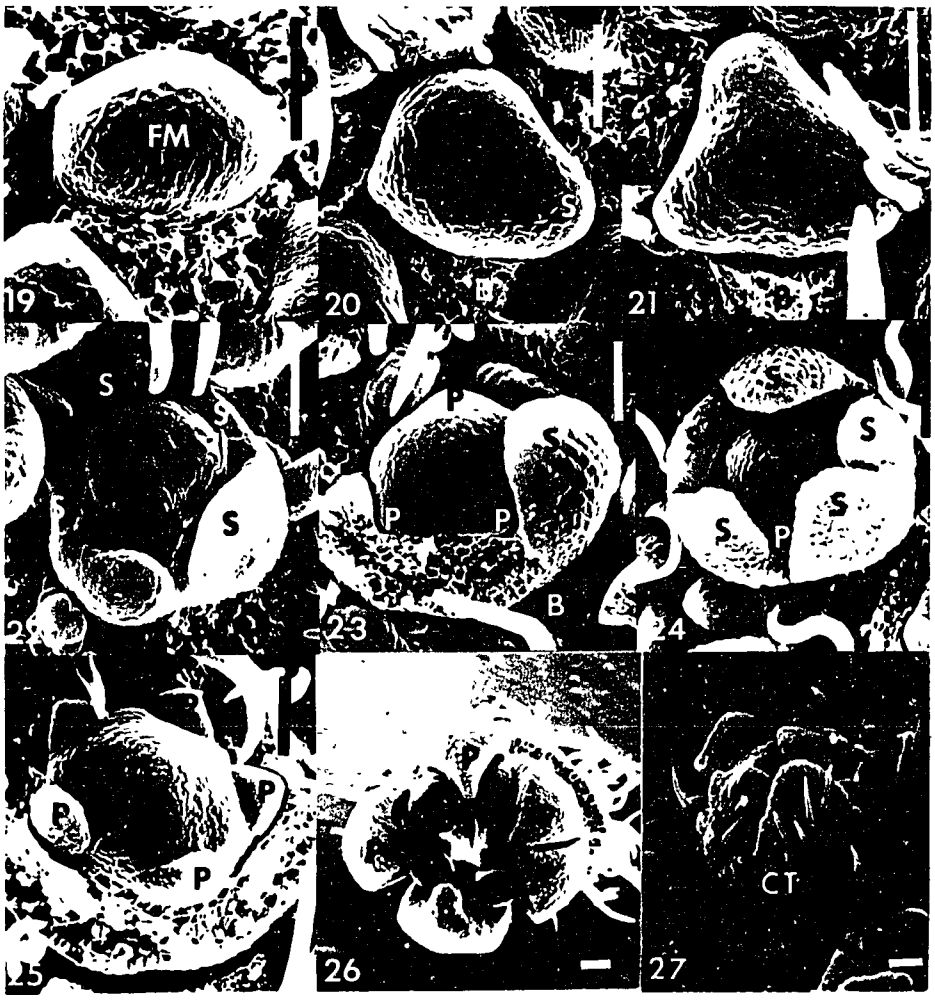
Figs. 19-27. Flowers of Adenanthera microsperma during early organogenesis and development of the perianth (SEM preparations). Subtending bract has been removed in all. Abaxial side is at base in all. Bar = 50 µm. 19. Polar view of bare flower meristem. 20-22. Stages during inception of five sepal primordia in a helical order of initiation. 23. Flower with one sepal removed during simultaneous inception of petal primordia. Only four primordia are shown here. 24. Polar view of flower showing imbricate aestivation of the calyx. 25. Synchronous enlargement of five petal primordia. Sepals have been removed. 26. Flower before anthesis. Three of five petals have been separated. Sepals have been removed. 27. Near-polar view of flower with calyx enclosing the bud in imbricate aestivation. B, bract; CT, calyx tube; FM, floral meristem; S, sepal; P, petal.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CT
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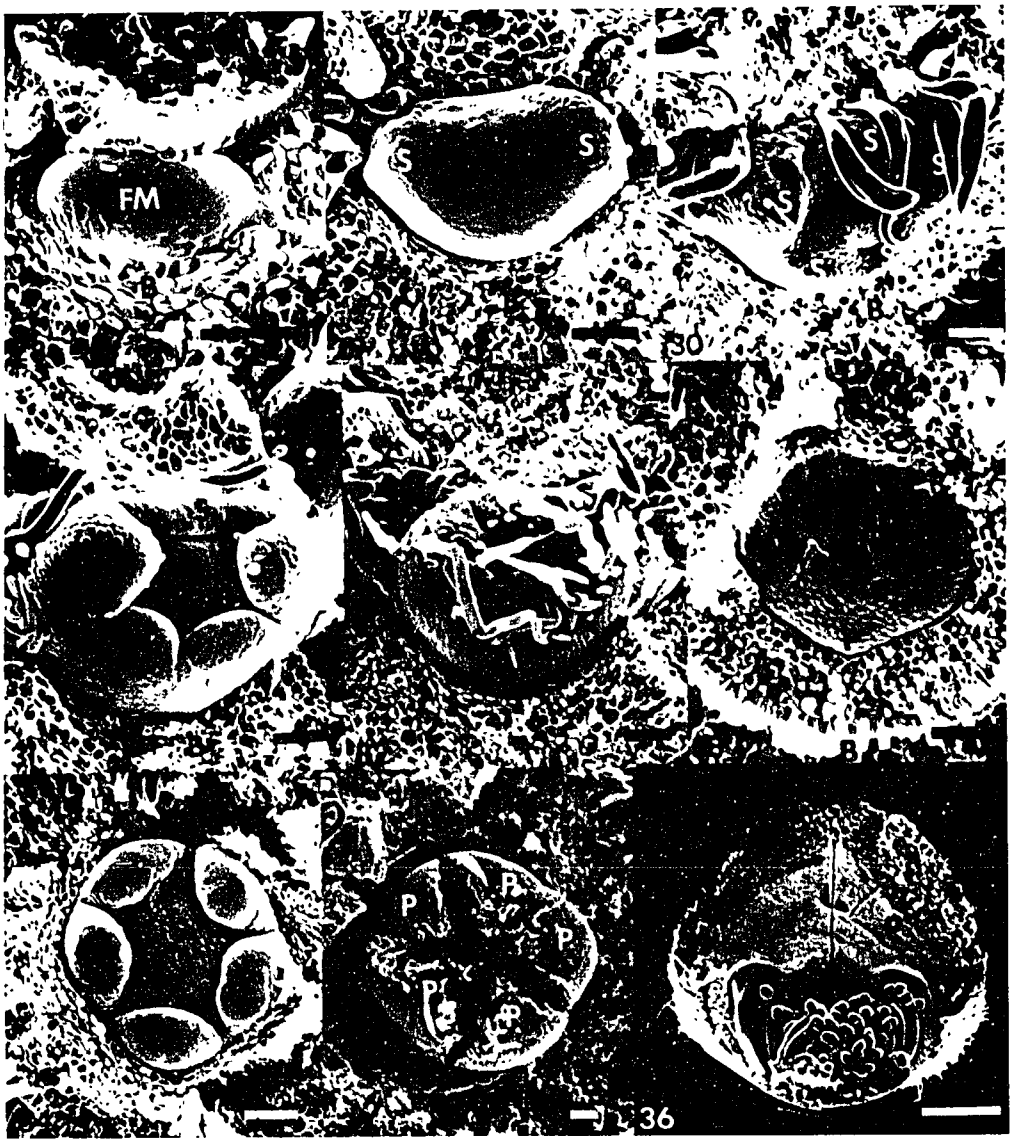
Figs. 28-36. Flowers of Wallaceodendron celebicum during early ontogeny and development of the perianth (SEM preparations). Subtending bract has been removed in all. Abaxial side is always at base. Bar = 50 µm. 28. Polar view of bare flower meristem. 29. Two sepal primordia are initiated simultaneously on opposite sides of the floral meristem. 30. Oblique view of flower with five sepal primordia. 31. Origin of calyx tube. 32. Hair-tipped lobes of the calyx tube enclose the flower bud in valvate aestivation. 33. Flower during initiation of the corolla. Sepals have been removed. 34. Polar view of flower with petals during early enlargement. Sepals have been removed. 35. Polar view of flower showing petals enclosing the bud in valvate aestivation. Sepals have been removed. 36. Side view of flower during late development. Three petals have been removed. Arrow indicates region of fusion between petals. B, bract; FM, floral meristem; S, sepals; P, petals.


FM
S
S
S
S
S
30
P
P
P
P
36

Figs. 37-42. Flowers showing different orders of calyx initiation (SEM preparations). Subtending bract has been removed in all. Abaxial side is at base. Bar = 50 μm. 37-38. Helical order of initiation with first sepal initiated in median adaxial position. 37. Acacia greggii. Polar view of flower during perianth initiation. 38. Acacia berlandieri. Flower at initiation of perianth. 39. Oblique view of Schrankia quadrivalvis at ring meristem initiation. 40. Polar view of Lysiloma bahamensis. Order of initiation is helical with first sepal initiated in abaxial position. 41. Near-polar view of Schrankia microphylla. Flower is six-merous. The calyx arises in a simultaneous whorl. 42. Polar view of flower of Acacia pinetorum with bidirectional order of initiation. B, bract; RM, ring meristem; S, sepal.

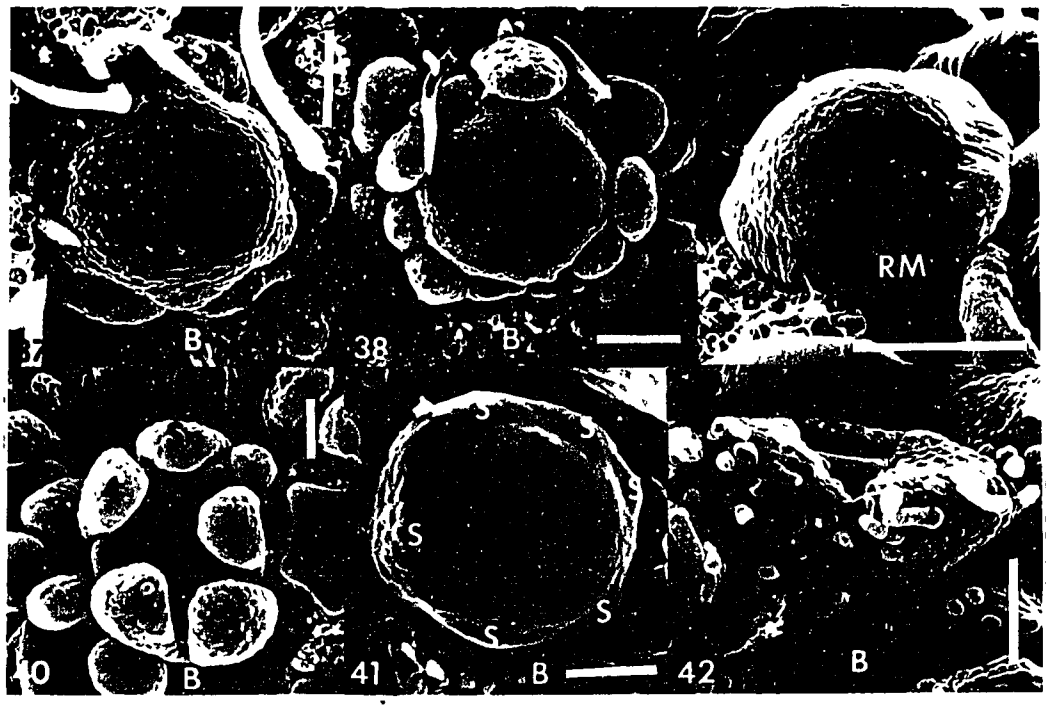
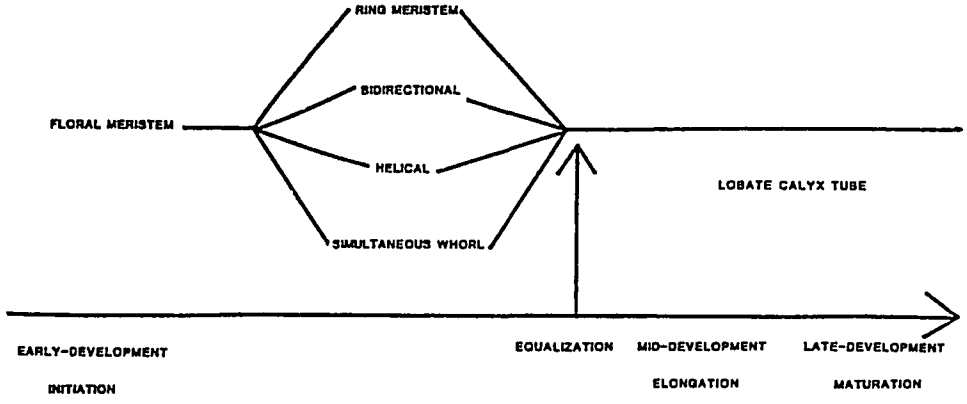

RM
B
38
S
S
S
S
S
40
B
41
B
42
B

Fig. 43. Diagram of ontogenetic events during calyx initiation and development seen among mimosoid legumes.


RING MERISTEM
BIDIRECTIONAL
FLORAL MERISTEM
HELICAL
SIMULTANEOUS WHORL
LOBATE CALYX TUBE
EARLY-DEVELOPMENT
INITIATION
EQUALIZATION
MID-DEVELOPMENT
ELONGATION
LATE-DEVELOPMENT
MATURATION

Comparative development of the androecium in Mimosoid Legume Taxa

Chapter 4

INTRODUCTION -- Androecial characters such as number and position of stamens are significant in classification and phylogeny among angiosperm families.

Development of the androecium in mimosoid legumes will be studied in order to determine variation and phylogeny of the androecium within the subfamily. Three main conditions; haplostemony, diplostemony and multistaminy are found among mimosoid legumes.

Opinions differ concerning how polyandry has arisen in evolution. In mimosoids, diplostemony has been considered a primitive condition and haplostemony and multistaminy have been considered derived (Gemmeke, 1982). Leins (1975) earlier proposed a different idea that diplostemony and haplostemony are derived conditions from a spiral type of multistaminate androecium through reduction, cyclisation and isomerization and from a complex androecium by reduction of parts. Ronse & Smets (1987) reported, based on several developmenta; work, five different conditions among multistaminous androecia in angiosperms: true polyandry (spiraly centripetal); complex centrifugal polyandry; complex centripetal polyandry; complex lateral polyandry and cyclic centripetal (or centrifugal) polyandry. They suggested that complex polyandry (multistaminy) may have probably arisen separately of a spiral type based on developmental evidence. One aim of the present research is to look for developmental evidence for or against these theories.

A second aim of this research is to compare ontogenetic patterns during early development of the androecium in mimosoids in order to determine relationships among and within the three major tribes.

Different patterns of development in multistaminous androecia are going to be analyzed in order to determine whether they represent parallelisms. Variations in patterns during early ontogeny have been suggested by Ramírez-Domenech & Tucker (1988) as examples of parallelism during development of the perianth among several mimosoid legumes (See Chapter 3).

MATERIALS AND METHODS -- Flower buds at different developmental stages were collected and fixed in FAA (formaldehyde-acetic acid-alcohol) solution. The species studied and their sources are listed in Table 1. Vouchers are deposited either in LSU herbarium or in the collectors personal herbaria. Each specimen was dissected in 95% alcohol. The material was then prepared for SEM as follows: dehydrated in an alcohol-acetone series, critical point dried in a DENTON-CP1 drying apparatus, mounted on stubs using colloidal graphite, coated with gold-palladium using a HUMMER II sputter coater. Observations were done using a Hitachi Scanning Electron Microscope. Photomicrographs were taken using Kodak Tri-X-Ortho film.

RESULTS -- Ontogeny of the androecium among mimosoid flowers is generally centripetal, with one exception known to occur in Acacia baileyana (Derstine, 1988) where the direction is centripetal and centrifugal. Symmetry of the androecium is always radial. Ontogenetic mechanisms during initiation of the androecium will be reported below for representative genera having each of the three conditions: haplostemony, diplostemony and multistaminy. The floral ontogeny of 22 species of mimosoids in three major tribes was examined and compared

(Table 1).

Haplostemony -- Haplostemony is rare in mimosoids, and occurs only in the tribe Mimoseae. A haplostemonous androecium is recognized by having only one whorl of stamens at initiation. I studied only one species, Mimosa pudica, in the tribe Mimoseae, which is haplostemonous. However, haplostemony has been reported in Desmanthus illinoensis (Tucker, 1987) and some Neptunia species (Windler, 1966).

Mimosa pudica has radially symmetrical tetramerous flowers. The androecium initiates in a simultaneous whorl after inception of the corolla. Four stamen primordia arise synchronously (Fig. 1), free and equidistant in alternipetalous positions. The arrangement of the stamen sites is non-sagittal; that is, two stamens are abaxial and two adaxial in relation to the subtending bract. Mimosa is unlike other mimosoids in that sepals grow unevenly and fused early, so are not used to indicate position (Ramírez-Domenech & Tucker, submitted).

Diplostemony -- Diplostemony is the predominant condition in the tribe Mimoseae. It is recognized by having two alternate whorls of stamens during development of the androecium. Diplostemonous development has been described in Mimosa strigillosa (Ramírez-Domenech & Tucker, in press), Neptunia pubescens (Tucker, 1988), Adenanthera pavonina and Leucaena leucocephala (Gemmeke, 1982).

In Mimosa strigillosa the androecium consists of eight stamens in two alternating whorls of four stamens. The first whorl of stamens is in alternipetalous position (Fig. 2) and the second whorl of stamens is antepetalous (Fig. 3).

Development of this species has been described in detail in Chapter 2 (Ramírez-Domenech & Tucker, in press). The antesepalous stamens are initiated after sepals and petals, and antepetalous stamens last. At initiation, individual stamen primordia arise free, equidistant and simultaneously per whorl (Fig. 2). Inception of the second whorl of stamens is preceded by initiation of the carpel as a circular mound in the center of the flower (Fig. 3). Similar floral development was found in Mimosa pigra (Fig. 4), Leucaena leucocephala (Fig. 5), Calpocalyx dinkaglei (Fig. 6) and Dichrostachys cinerea (Fig. 7). The last three have five-merous flowers with an androecium of ten stamens in two alternate whorls (antesepalous, antepetalous). Other merosities were found in Mimosa caesalpinifolia (trimerous) and Schrankia microphylla (regularly six-merous).

Multistaminy -- The androecium in multistaminous mimosoid flowers is radially symmetrical at initiation and development. I recognize five mechanisms of development during early ontogeny of mimosoids, including that described by Derstine (1988). Three of the four patterns (lateral multistaminy, acropetal multistaminy, and sectorial) are similar at first in having a whorl of five common primordia at initiation but differ thereafter. The direction of stamens during proliferation serves as a basis to distinguish among patterns. "Lateral multistaminy" is characterized by lateral inception of stamens preceding acropetal inception. An "acropetal" pattern characterizes stamens proliferating first acropetally and then others being added laterally. In the "sectorial" pattern stamens arise acropetally in clusters and

then others are added laterally in sectors. The "helical" pattern differs from the previous three, by having some stamens arising helically. All stamens in each species studied are eventually equalized in size, making it impossible to determine patterns of initiation after equalization.

I found two patterns of initiation of the androecium in the tribe Acacieae, in addition to the pattern reported by Derstine (1988).

One pattern found in Acacieae is lateral multistaminy, exemplified by Acacia smallii which has approximately 60-70 stamens in three rows. Five antesepalous primordia are initiated equidistantly, simultaneously and free (Fig. 10). The five points are found in the same arrangement as the outer stamen whorl of a diplostemonous mimosoid flower. The meristem expands laterally in diameter in a pentagonal shape (Fig. 11). Stamens are added first laterally from each of the five points or common primordia (Fig. 11). During this stage the carpel is demarcated as a circular mound in the center of the flower. Further addition of stamens proceeds acropetally (Fig. 12) to produce three rows of stamens eventually (Fig. 13).

Other examples of this pattern of development are found in Acacia berlandieri (Fig. 14) and Acacia greggii (Fig. 17). The floral meristem is more convex at inception of the first stamens in Acacia berlandieri (Fig. 14) than in Acacia smallii. The receptacle increases in height and width when stamens are added acropetally and laterally (Fig. 15) to eventually complete 3-4 rows of stamens (Fig. 16). The carpel arises in the center of the flower after most of the stamens are present (Fig.

15). In Acacia greggii the receptacle expands laterally than upward enclosing the carpel in a pit (Fig. 17). The stamens are initiated in acropetal sucession in about 3-4 rows of stamens (Fig. 18).

A second pattern of development, sectorial, is found in Acacia retinoides and Acacia pinetorum. The androecium in Acacia retinoides has about 100-120 stamens in at least five rows. Five antesepalous common stamen primordia arise simultaneously, equidistant and free, in the same arrangement as the outer whorl of diplostemonous flowers. Five clusters of stamens develop at each of the five points or common primordia (Fig. 19). The floral meristem thereafter expands laterally and increases in height (Compare Fig. 19 and 20). Inception of stamens proceeds acropetally producing a cluster of stamens at the area of each common primordium (Fig. 20). The sectors between the clusters later show a delay before they become filled in with additional stamens (Fig. 21). Another species with similar development is Acacia pinetorum (Figs. 22-24) with about 40-50 stamens in three rows. Stamens arise in clusters at five points (Fig. 22). Addition of stamens is first acropetal and then lateral in each cluster (Fig. 23). Sectors between each cluster are later filled in laterally with additional stamens (Fig. 24).

Six representative genera among the tribe Ingeae (Zapoteca portoricensis, Pithecellobium unguis-cati, Inga vera, Lysiloma bahamensis, Wallaceodendron celebicum, Albizia polyphylla) were studied, which include three patterns of development to be described below.

The first type is shown in Zapoteca portoricensis and

Pithecellobium unguis-cati. The pattern of acropetal multistaminy is different from those described for Acacieae in that proliferation of stamens proceeds first acropetally and then laterally. Zapoteca portoricensis has a total of about 50-70 stamens in four rows. During initiation five antesepalous common primordia arise at five equidistant points (Fig. 25). Proliferation of stamens is preceded by lateral expansion of the meristem. Stamens are first added acropetally (Fig. 26) and then laterally. The meristem increases slightly in height during this stage as the carpel is initiated (Fig. 27). The carpel is a circular mound in the center of the floral apex. Further addition of stamens proceeds acropetally and laterally (Fig. 28) to eventually produce four rows of stamens (Fig. 29).

Another example showing this type of initiation is Pithecellobium unguis-cati. Five antesepalous stamens are initiated simultaneously at five points. Addition of stamens proceeds when the first stamens are added acropetally and then accommodating additional stamens laterally (Fig. 31) and eventually two whorls of stamens are present (Fig. 32).

A second type of initiation of the androecium, lateral multistaminy, is found in Inga vera, Lysiloma bahamensis and Wallaceodendron celebicum. This pattern is similar to one type seen in Acacieae.

In Lysiloma bahamensis the androecium consists of about 30 stamens. Five antesepalous primordia arise simultaneously at five equidistant points (Fig. 33). The meristem expands in diameter, after which stamens

are initiated laterally from the five antesepalous primordia (Fig. 34) and form a pentagonal ring-like structure (Fig. 35). Initiation of additional stamens proceeds in acropetal sequence eventually completing two rows of stamens (Fig. 36).

A lateral multistaminy type of initiation is also found in Inga vera (Fig. 40) and Wallaceodendron celebicum (Fig. 38). The meristem expands laterally and become flat and slightly concave in both species (Figs. 37, 40). In Wallaceodendron celebicum the surface of the meristem is demarcated with ridges that connect the five antesepalous stamen primordia to the center of the apex (Fig. 38). Proliferation of stamens is first laterally from each of the common primordia in a pentagonal ring-like structure (Fig. 37) and then acropetaly from each of the points (Fig. 38). The receptacle in Inga vera after organogeny is fully covered by stamens (Fig. 41). In Wallaceodendron celebicum there is a space (which may become nectariferous) between the last whorl of stamens and the carpel (Fig. 39).

A unique type of stamen organogeny, helical, is seen in Albizia polyphylla with a total of about 25-30 stamens. This species is unique among other species in that it produces a second group of petals, usually five or six (Fig. 42), and the carpel is off-center, with a larger bare area to one side (Fig. 44, 45). Five stamen primordia arise simultaneously in an antepetalous whorl (Fig. 42, 43). Stamens are added beginning from the five antepetalous points in helical succession (Fig. 43). The meristem expands in diameter and flattens as the additional stamens are initiated along a short helix (Fig. 44).

DISCUSSION -- Multistaminate androecium -- Phylogeny of the androecium in mimosoid tribes Acacieae and Ingeae has proceeded by proliferation in number of stamens. A previous report by Gemmeke (1982) on phylogeny of the androecium among mimosoids, hypothesizes that diplostemony is primitive and multistaminy and haplostemony derived. This idea was based on corespondence of position of the first stamen primordia in diplostemony with multistaminy and haplostemony. Our evidence however, suggests that multistaminy and diplostemony are derived conditions from haplostemony (Fig. 46) based on phylogenetic analysis using two methods of polarization.

Mimosoids are generally considered monophyletic (Polhill et al. 1981). I used two methods of polarization for androecial characters: ontogenetic evidence and outgroup analysis.

One whorl of stamens is considered primitive by both methods. Ibelieve that stamen proliferation is derived. The ontogenetic evidence indicates that multistaminy has probably occurred through radial expansion and increase in height of the meristem, shown in the present work and in Derstine (1988). Both mechanisms provide more surface on which stamens can be added. Expansion of the meristem was shown during addition of stamens in species in Acacia (Newman, 1936; Derstine, 1988) and in Ingeae (Sattler, 1973; Gemmeke, 1982). Tucker (1960) showed that an increase in meristem size occurred through time of initiation of stamens in Michelia fuscata in Magnoliaceae. A similar developmental mechanism is reported among 21 genera of palms, in which polyandry involves expansion of the meristem after origin of the petals

(Uhl, 1988).

Polarization of androecial characters using outgroup comparison method was followed using Gleditsia as a sister group. The outgroup comparison method (indirect method) is considered the most useful in phylogenetic analysis (Humphries and Funk, 1984). An outgroup (sister group) is selected and used in polarization of character states. Characters that occur in both, the sister group and the study group, are considered primitive and those that occur only in the study group are derived. Flowers of Gleditsia have been considered the most primitive among legumes (Dickison, 1981). Polhill et al. (1981) mentioned that mimosoids and caesalpinioids are closely related based on similarities in floral morphology among the Gleditsia group and Dimorphandra group and mimosoid taxa. The androecium of Gleditsia is haplostemonous, with helical initiation of stamens (Tucker, in prep). Since the androecium of Gleditsia is simple, in that it has only one whorl of stamens, diplostemony and multistaminy are considered derived.

Multistaminy among angiosperms -- Mimosoids are only one of several families or subfamilies showing multistaminate evolution among angiosperms. Multistaminous androecia are found in about 75 families of angiosperms (Heywood, 1985).

Multistaminy may occur with order of stamen initiation either centripetal (common, ie in Magnoliaceae) or centrifugal (as in Palms). Centrifugality occurs rarely in mimosoids. Derstine (1988) found that in Acacia baileyana stamen initiation is partly centrifugal and mostly centripetal. Proliferation of stamens proceeds acropetally

first and then additional stamens are added basipetally. Corner (1946) studied centrifugal stamens in 13 families among angiosperms. Four patterns were found: 1) initial whorls 2) centrifugal fascicles 3) zonation and 4) centrifugal obdiplostemony. Tucker (1972) surveyed centrifugal androecia among angiosperms and reported 32 families with centrifugal inception of stamens. It was suggested that centrifugal order in the androecium has occurred more than once in phylogeny of angiosperms. Centrifugal development of stamens is reported for Arecaceae in Phytelephantoid palms (Uhl & Moore, 1977). Developmental studies among three genera (Palandra, Phytelephas, Ammendra) indicated a different method of expansion of the floral apex to accomodate stamens. In Palandra, the stamen inception occurs in radial rows along ridges from the edges of the floral apex. Phytelephas differs from Palandra in having sequential inception of stamens. The stamens arise in an irregular ring around the floral apex and subsequent ones in irregular order around the edges of the apex. Centrifugal order of stamen initiation has not been a major trend in mimosoids, based on its rarity in published reports and in my work.

Different development patterns of the androecium which combine centrifugal and centripetal inception of stamens are found in Eucnide (Loasaceae). Hufford (1988) found that in E. cordata, E. baronioides, E. urens and E. hirta inception of early stamens is first lateral and then acropetal and basipetal. Another pattern was found for E. aurea in which the androecium arises in four whorls of five stamens in acropetal succession. In E. bartonioides different patterns during

proliferation were found based on stamen position during inception. A similar pattern which combines centripetal and centrifugal initiation is found in Acacia baileyana (Derstine, 1988).

Centripetal development of the androecium in Rhizophoraceae shows some similar patterns to those in some mimosoid taxa. Juncosa (1988) thinks that multistaminy evolved independently in the genera Crossostylis, Cassipourea and Kandelia. A pattern not found in mimosoids is that in which multistaminy occurs in only one whorl of stamens that arises simultaneously. In Crossostylis grandiflora 25-30 stamens were found to arise simultaneously in a whorl. The androecia in several species of Cassipourea may be diplostemonous or multistaminate. In one multistaminate species studied all stamen primordia were found to initiate simultaneously around the margin of the floral apex as in Crossostylis. A pattern similar to the sectorial pattern, found in Acacieae, was reported for Kandelia. The stamens arise from common primordia forming sectors.

Leins (1975) thougth that complex polyandry among angiosperms, such as in mimosoids and several other families or subfamilies, is primitive, and that diplostemony and haplostemony are derived from a complex androecium by reduction of the parts or by reduction, cyclisation and isomerization, from a spiral type of androecium. However, Gemmeke (1982) suggested that within mimosoid taxa multistaminy and haplostemony are derived and diplostemony is primitive. My work, however, suggests a different alternative for phylogeny of multistaminy in mimosoids. Multistaminy may have probably arisen from a

diplostemonous type which in turn may have arisen from haplostemony by increasement in number of parts.

Order of initiation -- Order of initiation of stamens distinguishes the tribe Mimoseae from the other two tribes studied (See Table 2). Two main types of order of initiation are: 1) simultaneous whorl, and 2) simultaneous in a first whorl with acropetal, basipetal, or lateral proliferation. Simultaneous initiation per whorl is found in haplostemonous and diplostemonous androecia of Mimoseae. In multistaminous androecia the first whorl of stamens corresponds to the first whorl in a diplostemonous androecium, but later stamens initiate in new patterns or arrangements.

Developmental data in diplostemony is reported for Mimosa strigillosa (Ramírez-Domenech & Tucker, in press), Adenanthera pavonina, Leucaena leucocephala (Gemmeke, 1982) and Neptunia pubescens (Tucker, 1988). Multistaminy in mimosoids is complex and varies developmentally. Different patterns during development have been reported for several species in the tribes Acacieae and Ingeae. Derstine (1988) studied multistaminy in Acacia baileyana. Five common primordium are found to arise simultaneously, followed by proliferation of stamens acropetally first and then additional stamens basipetally. Other species of Acacia show different patterns. Newman (1936) found that, in Acacia suaveolens and Acacia longifolia, proliferation of stamens proceeds acropetally, from an area on the floral apex he called the "shoulder". Gemmeke (1982) described a pentagonal primordial ring in Acacia neriifolia. First stamens are initiated laterally in a

meristematic ring ("Ringwall"), and others are then initiated acropetally. Of the patterns reported among species in Acacieae, two are also found in Ingeae. Sattler (1973) reports a pattern similar to that described by Newman (1936), in Albizia lophantha. Previous reports on Albizia lophantha emphasized the position of common primordia and mentioned the proliferation of stamens in acropetal succession forming whorls (Hirmer, 1916). However, Gemmeke (1982) determined a different pattern in Albizia lophantha from the descriptions by Sattler (1973) and Hirmer (1916). A pentagonal primordial ring was described by Gemmeke (1982) for both Acacia neriifolia and Albizia lophantha. In another pattern, found in Lysiloma vogelianum, the stamens originate from 5 episepalous primary primordia followed by acropetal and lateral inception of stamens (Gemmeke, 1982).

Variations in patterns of initiation of the multistaminate androecium represent different developmental mechanisms (Fig. 46). Four patterns are found among the species studied: 1) lateral multistaminy, 2) sectorial, 3) acropetal multistaminy and 4) helical. Gemmeke (1982) described only two patterns, five antesepalous primordia and a pentagonal primordial ring, for three genera (Lysiloma, Albizia, Acacia) studied. Her five antesepalous primordia pattern corresponds to the acropetal multistaminy type in my terminology. A pentagonal primordial ring was not observed in any plants in our study. Derstine (1988) described another pattern for Acacia baileyana with five simultaneous antesepalous stamens first, and then lateral, acropetal and basipetal inception of additional stamens. A pattern similar to

acropetal multistaminy was found in Acacia suaveolens and Acacia longifolia by Newman (1936) and in Albizia lophantha by Sattler (1973) and Hirmer (1916).

Helical initiation found once in Ingeae is considered derived and advanced on the bases of polarization using ontogenetic evidence and outgroup comparison methods.

Distribution of variation among multistaminate flowers of Ingeae is represented in Table 2. A lateral multistaminy type is found in both tribes Acacieae and Ingeae. The sectorial type has been found only in Acacieae and the acropetal multistaminy type and helical type initiation only in Ingeae.

Tribal distinctions -- The two multistaminate tribes differ in whether stamens are fused (Fig. 46). This fusion occurs late in development. Stamens remain free in Acacieae and fused into a staminal tube in Ingeae (Elias, 1981).

Acacieae and Ingeae probably shared early evolution but separated when fusion was introduced in Ingeae (Fig. 46). Several genera and species of both tribes, Acacieae and Ingeae, are represented in tropical America, Asia, Africa and Australia (Elias, 1981). Elias (1981) suggests that Acacieae and Ingeae are more specialized and of more recent evolution than other mimosoid tribes. Character states such as pollen shed in complex polyads, adaptation of flowers for bird and bat pollination, connation of stamens, increase in stamen number and inflorescences with andromonoecious flowers are considered specialized, and are characteristic in Acacieae and Ingeae.

Other tribes in Mimosoideae not included in this study are Mimozygantheae and Parkieae. Flower material has not been obtained for genera within those tribes. Mimozygantheae is monotypic, with only one species, Mimozyganthus carinatus (Elias, 1981). Flowers are five-merous with imbricate sepals, valvate petals, with the androecium consisting of ten stamens. Parkieae consists of two genera: Parkia and Pentaclethra. Flowers are characterized by imbricate sepals united into a calyx tube and five to ten stamens with staminodia (Elias, 1981). Both tribes Parkieae and Mimozygantheae have been considered derived but less specialized than the three major tribes studied.

Common primordia -- In most multistaminous androecia development is initiated by five common primordia. Proliferation of stamens occurs from these five equidistant points that arise simultaneously after inception of the petals. Derstine (1988) described common primordia based on histogenetic study during initiation of the androecium in Acacia baileyana. Discrete portions of the floral meristem producing multiple stamens were recognized at five equidistant points on the flanks of the meristem. Stamens proliferate acropetally, laterally and basipetally in this species. Common primordia have also been found during development of the androecium in two genera of palms, Beccariophoenix and Polyandrococos, (Uhl, 1988) where thre stamens are initiated in antesepalous position with subsequent development in rows along acropetal ridges.

Carpel -- Relative time of initiation of the carpel may vary among multistaminous mimosoid flowers. Generally the carpel arises after

inception of the five common primordia in Acacieae and Ingeae and after most all of the first whorl in Mimoseae are present. Time of initiation of the carpel during early ontogeny of the androecium in multistaminous flowers corresponds to that in diplostemonous flowers. The difference probably lies in that there is continued meristematic capacity around the base of the carpel in multistaminate flowers.

Parallel evolution -- Different patterns of initiation of the multistaminate androecium may be an example of parallelism. During early ontogeny pathways occur that however result in similar morphologies (Fig. 46). In Figure 46, types of variation among multistaminous androecia are recognized as different lines which eventually converge during equalization. At this point, different morphologies detected during early development are unrecognized due to stamen growth and development of the androecium on the receptacle. In the diagram only few stamens are shown in multistaminy around one of the five common primordia. Diplostemony (Fig. 46C) is indicated to arise from haplostemony (Fig. 46B) through an increase of stamens arranged in two whorls.

The different pathways yielding multistaminy, are non-terminal at one point during development, similar to the different pathways for calyx order (Ramírez-Doemench & Tucker, 1988). These non-terminal pathways in development are important because examples in plants are rare. Moreover, it has been mentioned that non-terminal insertions in pathways may not be usable to infer phylogenies (Gould, 1977; de Queiroz, 1985).

Alberch (1985) stated that situations during development where different patterns occur at one point of ontogeny are insignificant perturbations. Our evidence however, suggests that differing patterns during initiation of the androecium are more than just "insignificant" variations. Each type (character state) results from an independent pathway which results in multistaminy. Moreover, each type is genetically controlled and characteristic for a particular species. During ontogeny divergent pathways are equalized resulting in similar morphologies. Equalization occurs when all stamens are uniform in size, and consequently each pattern at initiation is not detected.

Another example of parallel evolution was described in perianth ontogeny among several mimosoid taxa (Ramírez-Domenech & Tucker, 1988). Four types of order of sepal initiation were found. Similar morphologies late in development resulted from subsequent equalization. Each type of calyx initiation represents a different character state.

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Table 1. List of genera and species studied.

Species name	Source	Collector and number
Tribe: Mimoseae		
Mimosa pudica L.	Berkeley, California	Ramírez, 2049
Mimosa pigra L.	Tabasco, Mexico	Lievens & Gregory 2322
Mimosa albida H. & B. ex Willd.	Tabasco, Mexico	Lievens & Gregory 3116
Mimosa strigillosa Torr. & Gray	Baton Rouge, La.	Ramírez, 1002
Mimosa caesalpinifolia Benth.	Fairchild Trop. Gard. Miami, Fla.	Tucker, 25182
Schrankia quadrivalvis (L.) Britt. & Rose	Tabasco, Mexico	Lievens & Gregory 2321
Schrankia microphylla Dryand.	Fairchild Trop. Gard. Miami, Fla.	Tucker, 26495
Leucaena leucocephala (Lam.) de Wit.	Cabo Rojo, P. R.	Ramírez, 1005
Calpocalyx dinkaglei Harms.	Royal Bot. Gardens Miami, Fla.	Tucker, 24842
Dichrostachys cinerea (L.) W. A.	Tucson, Arizona	Gilberson s. n.
Desmanthus virgatus (L.) Willd.	Sinaloa, Mexico	Luckow, 2989

Continuation table 2.

Tribe: Acacieae		
Acacia smallii Isely	Baton Rouge, La.	Ramírez, 1007
Acacia pinetorum Benth.	Fairchild Trop. Gard. Miami, Fla.	Ramírez & Lievens 2026
Acacia berlandieri Benth.	Hidalgo County, Tx.	Lievens, 3017
Acacia greggii Gray & Wright	Santa Barbara Bot. Gard., California	Tucker, 28786
Acacia retinoides Schlecht.	Royal Bot. Gardens Kew, England	Tucker, 24696
Tribe: Ingeae		
Zapoteca portoricensis (Jacq.) H. Hernandez	Royal Bot. Gardens Kew, England	Tucker, 24698
Pithecellobium unguis-cati (L.) Benth.	Fairchild Trop. Gard. Miami, Fla.	Tucker, 25476
Inga vera Willd.	Veracruz, Mexico	Lievens & Gregory 3089
Lysiloma bahamensis Benth.	Fairchild Trop. Gard. Miami, Fla.	Ramírez & Lievens 2038
Wallaceodendron celebicum Koord.	Fairchild Trop. Gard. Miami, Fla.	Ramírez & Lievens 2048
Albizia polyphylla Fourn.	USPIS, Miami, Fla.	Tucker, 25490

Table 2. Distribution of order of initiation and types of variation during development of the androecium.

GENERA	TYPE OF ANDROECIUM	ORDER OF INITIATION
Tribe: Mimoseae		
Mimosa pudica	h	1
Mimosa pigra	d	2
Mimosa albida	d	2
Mimosa strigillosa	d	2
Mimosa caesalpinifolia	d	2
Schrankia quadrivalvis	d	2
Schrankia microphylla	d	2
Leucaena leucocephala	d	2
Calpocalyx dinkaglei	d	2
Dichrostachys cinerea	d	2
Desmanthus virgatus	d	2
Tribe: Acacieae		
Acacia smallii	m	3
Acacia pinetorum	m	4
Acacia berlandieri	m	3
Acacia greggii	m	3
Acacia retinoides	m	4
Tribe: Ingeae		
Zapoteca portoricensis	m	5
Pithecellobium unguis-cati	m	5
Inga vera	m	3

Continuation table 2.

Lysiloma bahamensis	m	3
Wallaceodendron celebicum	m	3
Albizia polyphylla	m	6

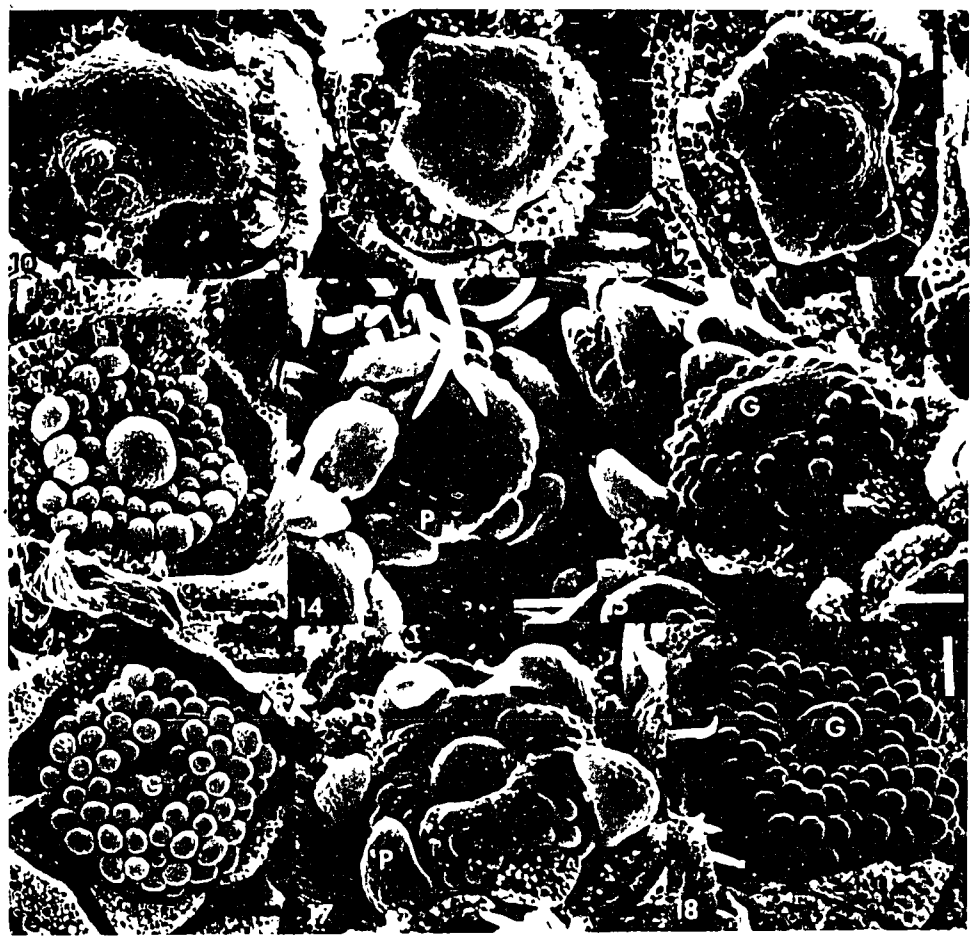
h, haplostemonous; d, diplostemonous; m, multistaminous; 1, simultaneous whorl; 2, simultaneous per whorl; 3, lateral; 4, sectorial; 5, acropetal; 6, helical

Figs. 1-9. Haplostemonous and diplostemonous stamen initiation. Flowers of different genera in the tribe Mimoseae during early ontogeny and development of the androecium (SEM preparations). The carpel is terminal in all. Calyx has been removed in all except in Figs. 1 and 4. Petals have been removed in all except in Figs. 1, 4, 5 and 9. Subtending bract is always at the base of each micrograph. Bar = 50 μm. 1. Mimosa pudica. Polar view of four-merous flower with only one whorl of stamens. 2-3. Mimosa strigillosa. 2. Polar view of flower during initiation of antesepalous whorl of stamens. The carpel is already visible at the center of the receptacle. 3. Polar view of flower during initiation of antepetalous whorl of stamens (at arrows). 4. Mimosa pigra. Polar view of flower with only first whorl of stamens present. Arrow indicates one of the four sites of inception of antepetalous stamen primordia. 5. Leucaena leucocephala. Near-polar view of flower with only the outer (antesepalous) whorl of stamens present. Arrow points to site for one of five antepetalous stamen primrodia. Only one petal and one antesepalous stamen are labelled. 6. Calpocalyx dinkaglei. Oblique view of flower with two (antesepalous, antepetalous) whorls of stamen present. Only one stamen for each whorl is labelled. 7. Dichrostachys cinerea. Polar view of five-merous flower with alternating whorls of stamens present. Arrow indicates 3 of the 5 antesepalous stamen primordia. 8. Mimosa caesalpinifolia. Polar view of trimerous flower after both whorls of stamens are present. Six stamens are present in two alternating whorls. 9. Schrankia microphylla. Oblique view of six-merous flower during early initiation of the androecium. Arrow

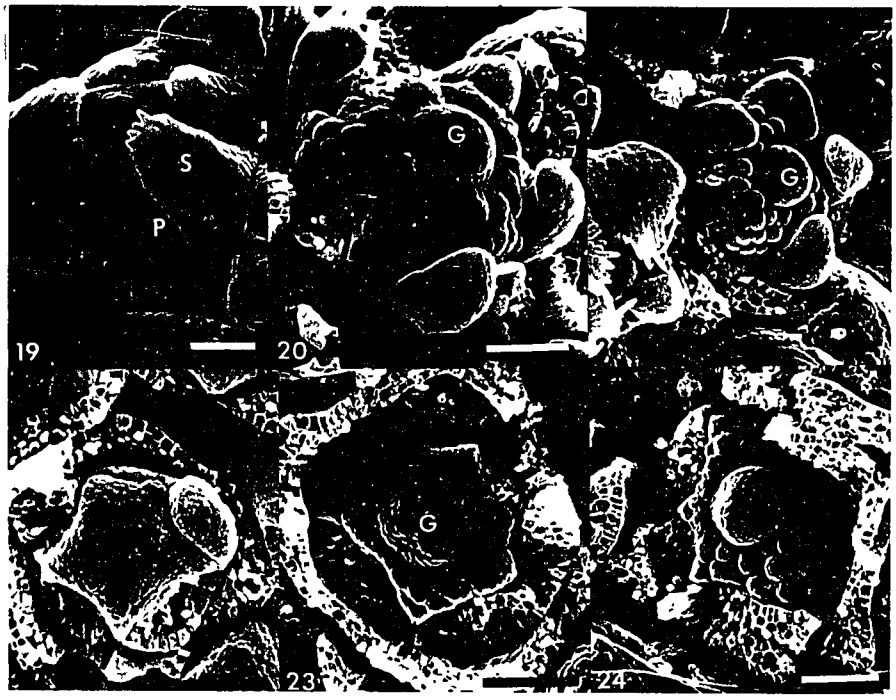
indicates one of the five antepetalous stamen primordia. Only one of the five antesepalous stamen primordia is labelled. AS, antesepalous stamens; ap, antepetalous stamens; C, calyx; G, carpel; P, petal.


P
AS
AS
C
AS
AS
2
AS
AS
C
AS
AS
3
C
AS
AS
5
ap
6
AS
AS
AS
G
AS
AS
AS
7
AS
ap
ap
AS
G
AS
ap
8
P
G
AS
9

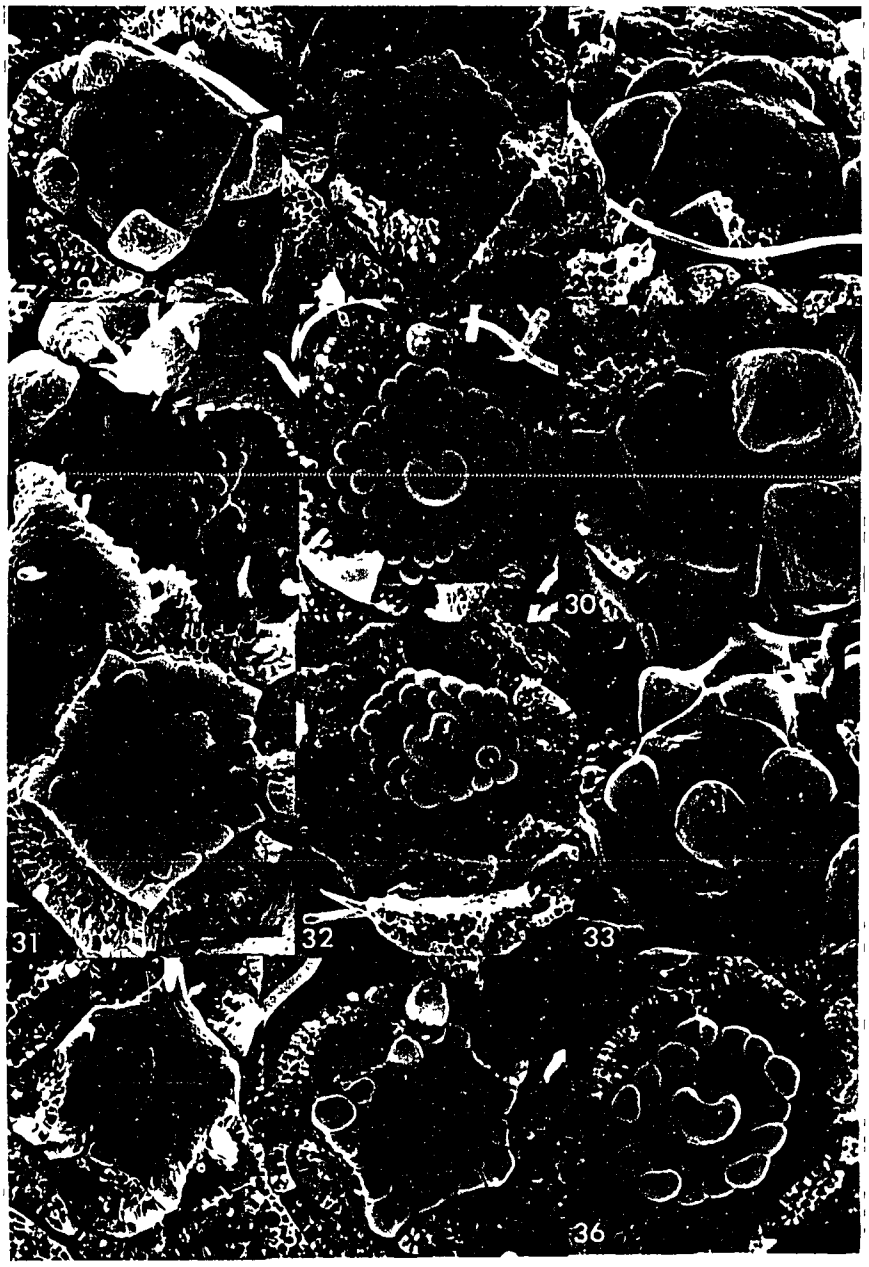
Figs. 10-18. Multistaminy. Early ontogeny and development of the androecium among species in the tribe Acacieae (SEM preparations). Bract is always at base. Sepals have been removed. in all except in Fig. 14. Petals have been removed in all except in Figs. 14, 15, and 17. Only one of the five petals is labelled. Bar = 50 μm. 10-13. Acacia smallii. 10. View of flower during stamen initiation. Five equidistant points (common primordia) are present (one shown at arrow). 11. Oblique view of flower showing lateral multistaminy order of initiation. 12. Polar view of flower during inception of second row of stamens. 13. Oblique view of flower with all rows present. 14-16. Acacia berlandieri. 14. View of flower during initiation of the androecium. Arrow points to common primordium site. 15. Side view of flower during initiation of the carpel and initiation of additional stamens around each stamen point. 16. Polar view of flower with about 110 stamens present. 17-18. Acacia greggii. 17. Side view of six-merous flower during addition of stamens. 18. Side view of flower with all stamens present. G, carpel; P, petal.


G
P
14
G
P
T
17
18

Figs. 19-24. Flowers of the tribe Acacieae during early ontogeny and development of the androecium (SEM preparations). Subtending bract is always at the base. Sepals have been removed in all except in Fig. 19. Petals have been removed in only Figs. 23-24. Bar = 50 μm. 19-21. Acacia retinoides. 19. View of flower during initiation of the androecium. Arrow indicates one of five primordia. 20. Oblique of flower showing clusters of stamens. Arrow points to bare sectors between two clusters of stamens. 21. View of flower with all stamens present. Arrow points at sector between two clusters of stamens. Figs. 22-24. Acacia pinetorum. 22. Polar view of flower with five common primordia present during initiation. Arrow points to one common primordium. 23. Polar view of flower during development of clusters. Arrow points at a stamen cluster. 24. Oblique view of flower with all stamens present. G, carpel; S, sepals; P, petals.


S
P
G
19
20
G
G
23
24

Figs. 25-36. Flowers of genera in the tribe Ingeae during early ontogeny and development of the androecium (SEM preparations). Sepals have been removed in all, and some petals removed in Figs. 25, 27, 28 and 30. Only one petal is labelled in each figure. Subtending bract has been removed in all and its scar is always at base of micrograph. Bar = 50 μm. Figs. 25-29. Zapoteca portoricensis. 25. Polar view of flower during inception of five common primordia. Arrow indicates one common primordium. 26. Side view of flower during first addition of stamen (at arrow) acropetal to the first initiated stamen. 27. Oblique view of flower with two petals removed. More stamens have been added laterally and acropetally in about three rows. 29. Polar view of flower showing about four rows of stamens occupying most of the surface of the receptacle. 30-32. Pithecellobium unguis-cati. 30. Oblique view of flower showing initiation of the androecium. Stamens are added first acropetally (at arrow). 31. View of flower showing lateral addition of stamens. The carpel has been initiated in the center of the flower. 32. Polar view of flower during development showing two rows of stamens. 33-36. Lysiloma bahamensis. 33. Polar view of flower showing five stamen primordia. 34. Polar view of flower showing lateral addition of stamens. Arrow points to one of the five first stamen primordia. 35. Flower showing pentagonal shape of the meristem during stamen inception. 36. Polar view of flower during development of the androecium with two rows of stamens present. G, carpel; P, petal.


30
31
32
33
36

Figs. 37-45. Flowers in the tribe Ingeae during initiation and development of the androecium (SEM preparations). Sepals have been removed in all. Petals have been removed in all except in Figs. 42-45. Only one petal in each flower is labelled. The subtending bract has been removed in all and is always at base of micrograph. Bar = 50 μm in all, except in Fig. 39 where bar = 500 μm. 37-39. Wallaceodendron celebicum. 37. Oblique view of flower showing initiation of the androecium. Five equidistant primordia of some sort arise simultaneously in a whorl. Arrow points to one stamen primordium. 38. Flower during lateral addition of stamens in a meristem with pentagonal shape. Five radial ridges are evident. 39. Side view of flower during late development, with half of flower removed. The carpel is terminal. A nectariferous disk is formed in an area between the carpel and the androecium (at arrow). Four rows of stamens are present. 40-41. Inga vera. 40. Oblique view of flower during initiation of stamens in a lateral multistaminy pattern, forming a pentagonal ring-like structure. Arrow indicates first stamen primordium. 41. Polar view of flower showing four to five rows of stamens. The carpel is terminal. 42-45. Albizia polyphylla. 42. Polar view of flower during inception of first stamen primordia. Two petals are labelled, one in each whorl (outer, inner). Arrow at stamen primordium. 43. View of flower during helical addition of stamens. Six inner petals are present (one labelled). Arrow at stamen primordium. 44. Oblique view of flower with proliferation of stamens around the floral meristem, on which the carpel is being initiated (at arrow). 45. Polar view of flower

showing complete androecium. Four stamens have been removed. Carpel is off-center in position. G,carpel; P, outer petal; p, inner petal.

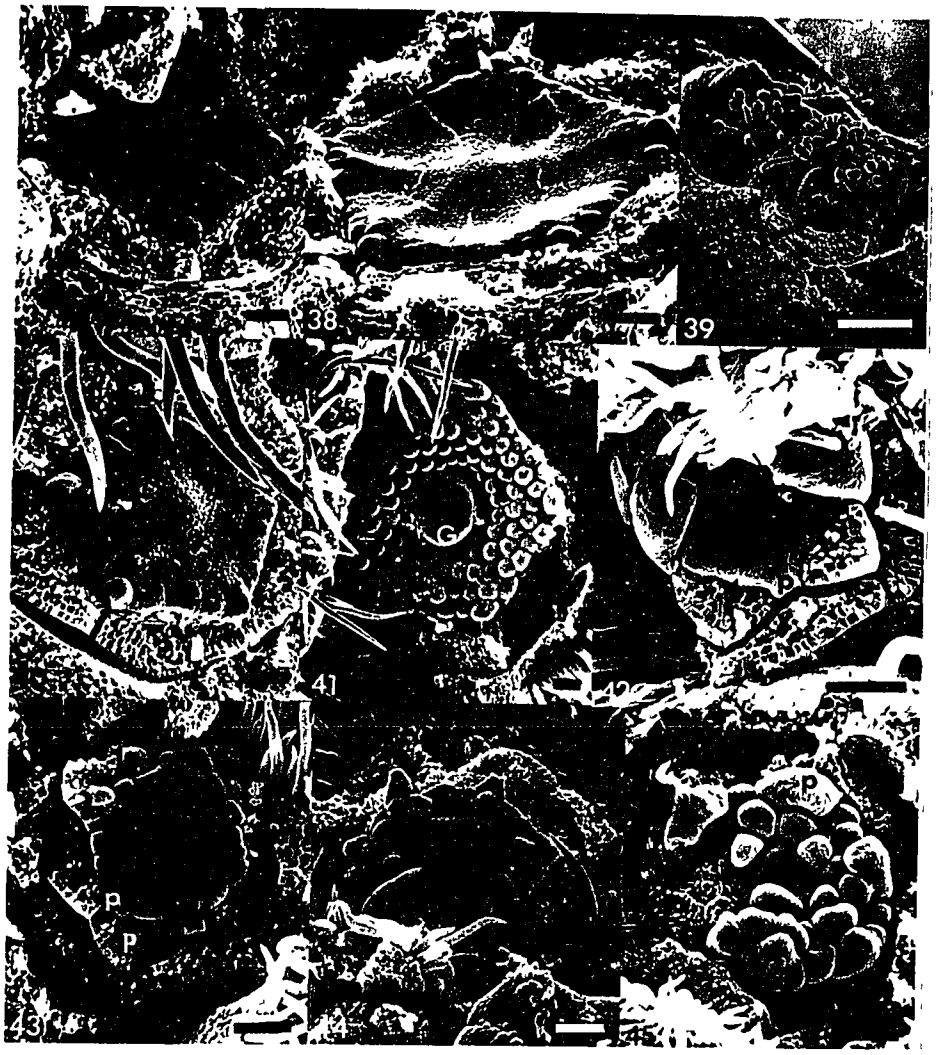
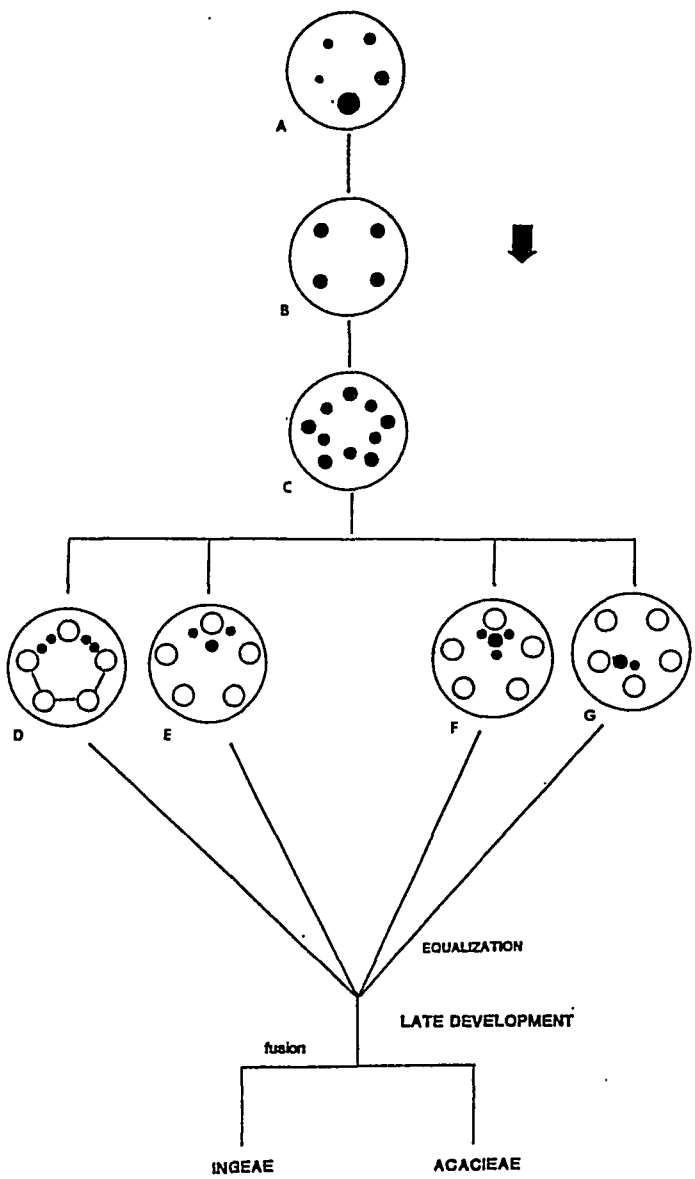

38
39
41
P
P
P
43

Fig. 46. Diagram illustrating a phylogenetic hypothesis for the androecium in mimosoid legume flower. Types of androecium shown are: A. helical in one whorl, B. haplostemonous, C. diplostemonous, D. lateral multistaminy, E. acropetal multistaminy, F. sectorial, G. helical


A
B
C
D
E
F
G
EQUALIZATION
LATE DEVELOPMENT
fusion
INGEAE
ACACIEAE

Summary

Chapter 5

SUMMARY

Comparative floral ontogeny of mimosoid legumes was studied for a total of 39 species, representing genera in the three major tribes Mimoseae, Acacieae and Ingeae. Important features analyzed include: order of perianth initiation, pattern of stamen initiation and proliferation, and position of organs.

All mimosoids share radial symmetry and acropetal inception of organs. Position of sepals and petals is a distinct taxonomic character, determined during early ontogeny, which separates the three subfamilies. In mimosoids the median sepal is adaxial and the median petal is abaxial in relation to the subtending bract. This pattern differs from the one observed in caesalpinioids and papilionoids in which the median sepal is abaxial and the median petal is adaxial in relation to the subtending bract.

The first chapter is a complete floral ontogenetic study of one mimosoid species, in which development of inflorescences and flowers is described and illustrated in detail. Ontogenetic analysis in Mimosa strigillosa explored the developmental basis for variation in number of parts, patterns of arrangement and inflorescence architecture. Each racemose inflorescence of M. strigillosa has acropetal order of initiation of bracts and flowers. Flowers later develop synchronously in the inflorescence except for the basal flowers which are retarded. It is suggested that suppression has been phylogenetically selected as a system to guarantee an optimal seed and fruit production. The calyx in flowers of M. strigillosa is unusual in that it arises as

a ring meristem, a specialized condition among mimosoids. Variability occurs in number of parts and may have evolved through reduction of a basic pentamerous structure, through fusion or suppression to tetramery. It is proposed that the number of parts and pattern of organ arrangement, in this genus, are correlated features.

Divergent patterns in order of initiation and development are found during 1) sepal initiation and 2) stamen initiation and proliferation. Four different types of order of sepal initiation found among 39 species of mimosoids studied are: helical, ring meristem, simultaneous whorl and bidirectional. The helical pattern is considered primitive on the base of outgroup comparison. Ring meristem, simultaneous whorl and bidirectional patterns are considered derived, on the basis of ontogenetic evidence. The differing patterns of sepal initiation occur at non-terminal points in floral development, yet the differences are not reflected in adult morphology. Equalization occurs when flowers with different order of sepal initiation become equal in size and morphology.

In the androecium, three main conditions (haplostemony, diplostemony, multistaminy) are found in the 22 species analyzed. Haplostemony and diplostemony are characteristic of the tribe Mimoseae (11 species) and multistaminy occurs in the tribes Acacieae (5 species) and Ingeae (6 species). Four different patterns of stamen initiation and proliferation found are: 1) lateral multistaminy, 2) acropetal multistaminy, 3) sectorial and 4) helical.

Different pathways yielding multistaminy also diverge at a non-

terminal point; non-terminal points in ontogeny have rarely been documented in plants. Our evidence suggests that multistaminy has evolved several times in mimosoids, each having a different pathway.

Ontogeny distinguishes tribes in such characters as order of stamen and fusion. Mimoseae is separated from Acacieae and Ingeae by having only haplostemonous and diplostemonous androecia. The other two tribes are multistaminate. The presence of common primordia at initiation of the androecium is characteristic of the tribes Acacieae and Ingeae. Ingeae is separated from Acacieae by fusion of stamens into a staminal tube, an event that occurs during late development.

The divergent patterns in order of sepal and stamen initiation probably are parallelisms among mimosoids. Each divergent line in sepal initiation and stamen initiation is considered a developmental pathway that represents a character state that can best be recognized during early ontogenetic stages. Some lines occur in more than one tribe. During late development in multistaminous androecia all parts of each whorl become equalized resulting in similar morphologies which obscure any divergences that have occured during early ontogeny.

Curriculum Vitae

Chapter 6

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Ramírez-Domenech, J. S. C. Tucker. 1988. Evidence for parallel evolution in mimosoid flowers. Amer. J. Bot. 75:42.

Ramírez-Domenech, J. & S. C. Tucker. 1987. Patterns of organ development in mimosoids. XIV Internat. Bot. Congress, Berlin, Ansts., p. 216.

Ramírez-Domenech, J. & S. C. Tucker. 1987. Primitive and specialized conditions of the androecium in mimosoid flowers. Amer. J. Bot. 74:623.

Ramírez-Domenech, J. & S. C. Tucker. 1986. Ontogeny of inflorescence and flowers in Mimosa strigillosa T. & G. Amer. J. Bot. 73:639.

Derstine, K. S. & J. Ramírez-Domenech. 1985. Significance of sepal and petal sites of mimosoid legumes. Amer. J. Bot. 72:812.

Publications:

Ramírez-Domenech, J. & S. C. Tucker. 1988. Patterns of organ development in mimosoid legume flowers. In: P. Leins, S. C. Tucker & P. K. Endress (eds.), Aspects of Floral Development. Gebruder Borntraeger, Berlin, Stuttgart. pp. 171-180.

Ramírez-Domenech, J. & S. C. Tucker. in press. Phylogenetic implications and floral ontogeny of Mimosa strigillosa. Amer. J. Bot.

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Major Field: Botany

Title of Dissertation: Floral Ontogeny of Mimosoid Legumes

Approved:

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Major Professor and Chairman

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